

INTRODUCTION

Anurans exhibit a diversity of reproductive modes, many of which are effective means of escaping partly or completely from the constraints imposed by aquatic eggs and larvae. Direct development of terrestrial eggs and the concomitant omission of aquatic larvae has evolved independently in many lineages, as witnessed by anurans having this reproductive mode in such diverse families as the Leiopelmatidae, Lepidodactylidae, Bufonidae, Hylidae, Ranidae, and Microhylidae. Thus, direct development of terrestrial eggs is a convergence in many anuran lineages. Studies on the embryology of diverse species having direct development have shown different developmental patterns and, especially important, different embryonic respiratory mechanisms, such as caudal tissue in lepidodactylids, lateral folds in platymantine ranids, and large gills in hylids.

The only hylids that have direct development brood their eggs on the dorsum or in a dorsal pouch of the female. All of these have large, bell-shaped gills that partly or completely envelop the developing embryo. This type of gill is unique to these frogs. Therefore, we may assume that the egg-brooding hylid frogs represent a monophyletic group. These frogs have been recognized as comprising the subfamily Amphignathodontinae (Duellman, 1970), with the exception that the osteologically bizarre, carnivorous frogs of the genus *Hemiphractus* have been accorded subfamilial rank—Hemiphractinae (Trueb, 1974).

The Amphignathodontinae contains six genera. Two of these—*Cryptobatrachus* (3 species) and *Stefania* (7 species) carry the eggs on the dorsum and have direct development; in these features they are like the five species of *Hemiphractus*. In the two species of *Fritziana* the eggs are carried in an open basin on the dorsum; they hatch into large, nonfeeding tadpoles. Females of the other genera of egg-brooding hylids have dorsal pouches in which the eggs develop into feeding tadpoles (some *Gastrotheca*), non-feeding tadpoles (*Flectonotus*), or froglets (*Amphignathodon* and some *Gastrotheca*).

In the absence of a brooding basin or

pouch, three genera can be considered generalized—*Cryptobatrachus*, *Stefania*, and *Hemiphractus*—although each is characterized by the absence of a free larval stage. *Hemiphractus* has been reviewed systematically (Trueb, 1974), and it is morphologically and behaviorally quite distinct from the other two genera. *Cryptobatrachus* currently is being studied by Pedro M. Ruiz-C. and María C. Ardila M. of Bogotá, Colombia.

The purposes of the present paper are to: 1) define the genus *Stefania*; 2) review the taxonomy of the species; 3) present accumulated information on the life history, ecology, and distribution of the species; and 4) assess the phylogenetic relationships of the species and the genus among amphignathodontine hylids.

The first mention of any of these generalized egg-brooding hylids is Boulenger's (1904) description of *Hyla evansi* from Guyana. The single female was carrying 22 eggs on the dorsum. Ruthven (1915) noted this brooding behavior in a Colombian frog referred to *Hyla fuhrmanni* Peracca. Ruthven (1916) named the genus *Cryptobatrachus* for these same specimens, for which he recognized a new species—*C. boulengeri*. In a review of the morphology and life history of egg-brooding hylids, Ruthven (1922) placed *Hyla evansi* Boulenger and *H. fuhrmanni* Perracca in the genus *Cryptobatrachus*. With the exception of Noble (1925), who placed these species in *Hyloscirtus* Peters (= *Hyla*; Duellman, 1970) but who recognized *Cryptobatrachus* in 1927, subsequent workers recognized the three species of *Cryptobatrachus*. Rivero (1968) concluded that *C. evansi* was generically distinct from the Colombian species and erected the genus *Stefania*; he also described three new species in the genus and transferred a species named as a *Hyla* to the genus. Rivero (1970) added another species to *Stefania*, and Cochran and Goin (1970) named a third species of *Cryptobatrachus*. Thus, at the present time *Cryptobatrachus* contains three species in the Andes of northern Colombia, whereas *Stefania* contains seven species in the Guianan region.

As part of a study of the egg-brooding hydrid frogs, Duellman examined type specimens of species of *Cryptobatrachus* and *Stefania* and collected specimens in Venezuela. In the course of a survey of the anuran fauna of the Guianan region, Hoogmoed accumulated data on *Stefania* in the field and from museum specimens (including the holotypes of all nominal species). In this paper we have combined our data to provide definitions of the genera and species, descriptions of two new species, and the relegation of one species to the synonymy of another.

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SYSTEMATIC REVIEW

GENUS *STEFANIA* RIVERO, 1970

Stefania Rivero, 1968:142. Type species, by original designation, *Hyla evansi* Boulenger.

Definition.—Moderate to large-sized hydrid frogs having great sexual dimorphism in

size ($\delta\delta$ to 57 mm, ♀♀ to 96 mm in snout-vent length); skull well ossified, exostosed or not, but never co-ossified; sphenethmoid well ossified anteriorly; prevomerine denticulous processes anterior to level of palatines (Fig. 1); maxillary teeth spatulate; choanae large, elliptical; vocal slits absent;

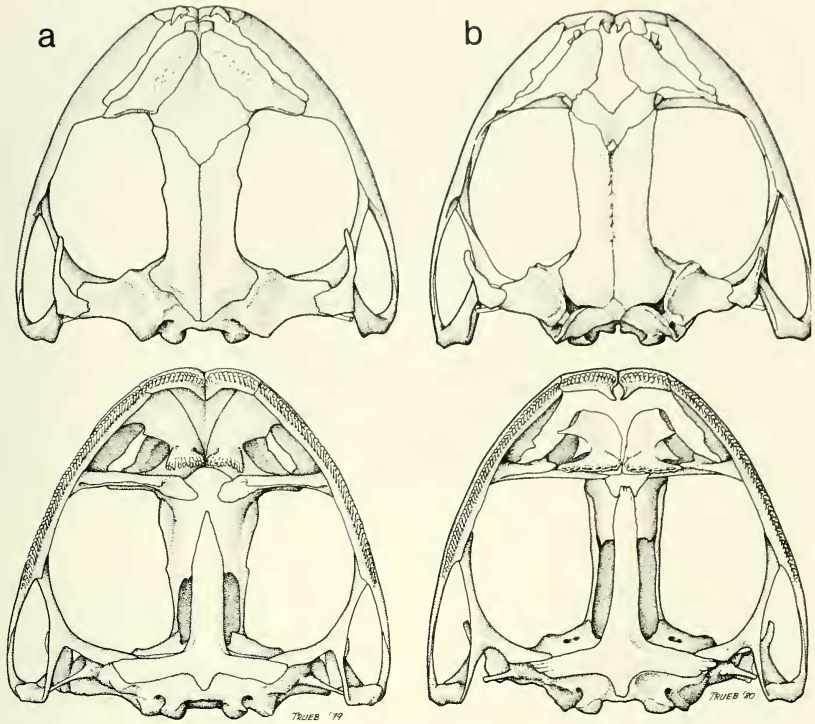


FIG. 1.—Dorsal and ventral views of skull of: a. *Stefania evansi* (KU 167671, ♀, 72 mm snout-vent). b. *Cryptobatrachus fuhmanni* (KU 169378, ♀, 57 mm snout-vent). Note particularly in the dorsal views the extent of ossification of the sphenethmoid anteriorly, and in the ventral views the positions of the dentigerous processes of the prevomers with respect to the palatines.

first finger longer than second; fifth toe longer than third; females brooding eggs on dorsum; eggs undergoing direct development into froglets; embryos completely enclosed in two pairs of gills; chromosome complement 13 pairs (known only in *S. evansi*).

Stefania is most similar to *Cryptobatrachus*, which differs from *Stefania* in having the sphenethmoid weakly ossified anteriorly, prevomerine dentigerous processes between palatines (Fig. 1), choanae small and ovoid, vocal slits present, first finger subequal to or shorter than second, fifth toe shorter than third, and embryos only partially enclosed in one pair of gills. The only other genus of hylids that brood individual

eggs on the dorsum is *Hemiphractus*, in which the head is triangular, skull extensively exostosed and co-ossified, and maxillary teeth fanlike.

Content.—Seven species—*S. evansi* (Boulenger), *S. ginesi* Rivero, *S. goini* Rivero, *S. marahuacuensis* (Rivero), *S. riae* new species, *S. roraimae* new species, *S. woodleyi* Rivero.

Distribution.—The genus is restricted to the Guianan Region of Guyana and Venezuela in northeastern South America. With the exception of *S. evansi* which has a broad distribution and is found in the lowlands as well as in the highlands, the species of *Stefania* have "insular" distributions on the slopes and tops of table mountains (tepuis) at elevations of 600 to 2450 m (Fig. 2).

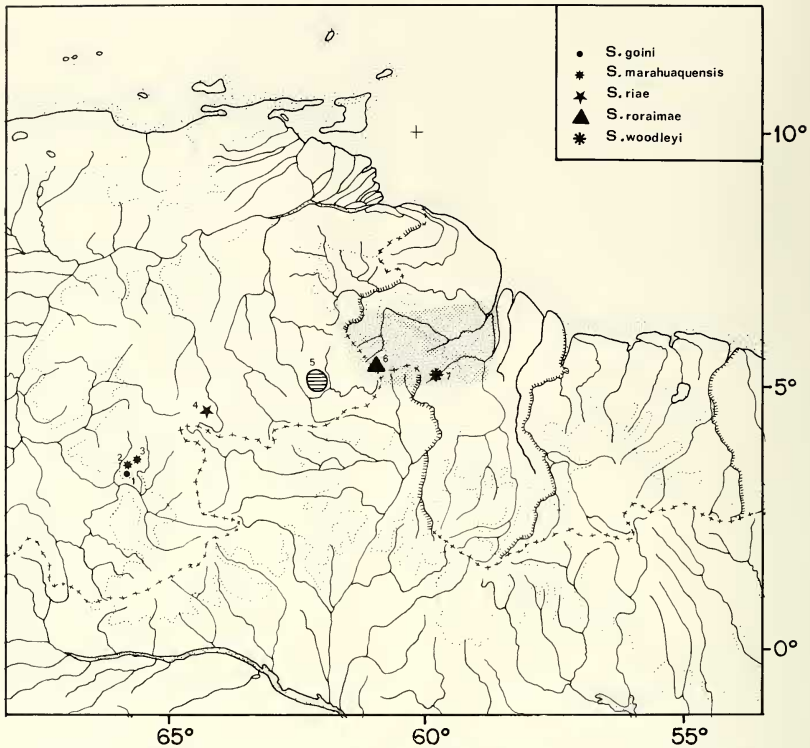


FIG. 2.—The Guianan Region of northeastern South America showing the distribution of the genus *Stefania*. The 200-m contour is indicated by dotted lines. Tepuis known to be inhabited by *Stefania* are: 1. Cerro Duida (Vegas Falls); 2. Cerro Duida (top); 3. Cerro Marahuaca; 4. Cerro Sarisariñama; 5. Auyán-Chimantá-tepui area; 6. Mount Roraima; 7. Mount Kanaima. The hatched area = *S. ginesi*; stippled area = *S. evansi*.

Reproductive Biology.—Females of three species of *Stefania* are known to brood eggs on their backs (Fig. 3); this life history trait is assumed to be characteristic of the entire genus and is shared with species of *Cryptobatrachus* and *Hemiphractus*. No observations have been made on amplexus or the method of placing the eggs on the backs of females in any of these genera. The young complete their development in the egg capsules and hatch as froglets.

The large eggs are in a single layer on the female's back. In *S. ginesi* the eggs are arranged in paravertebral rows, whereas in *S. evansi* and *S. goini* there is no distinct pattern to their arrangement. The external

capsules of the individual eggs are adherent to one another, but there is no common membrane covering the eggs. In those few females that were brooding eggs, a thin mucoid layer is present between the eggs and the skin on the dorsum. This layer apparently provides the adhesion of the eggs to the skin. Furthermore, the skin on the back of brooding females has pentagonal or hexagonal depressions, one for each egg (as examples, see Figs. 14 and 17).

Rivero (1970:463) noted that the mucoid layer in *S. evansi* “. . . is firmly attached to the mother's skin by the numerous spinulets with which it is studded.” Furthermore, he interpreted the mucoid layer to consist of



FIG. 3.—Female *Stefania evansi* (KU 167239) brooding eggs; photographed in life by W. E. Duellman.

two “membranes,” one possibly secreted by the female and the other by the eggs. The mucoid layer may be of dual origin, but most likely does not originate from the eggs. Hoogmoed (1967) noted that male *Gastrotheca riobambae* produce semen onto the back of the female and push the eggs across the semen into the pouch. Also, del Pino et al. (1975) observed that large secretory cells develop in the brood pouch in *G. riobambae* just before ovulation. The brood pouch of *G. riobambae* is formed by the invagination of the dorsal skin (Jones et al., 1973). It is reasonable to assume that the mucoid layer on the dorsum of brooding female *Stefania* is the result of the same kinds of processes that occur in *G. riobambae*: 1) at the time of mating the female secretes mucous from the glands in her dorsal dermis; 2) the male exudes semen on the mucous produced by the female; 3) as the eggs are extruded they are manipulated onto the female’s back, where they are fertilized; 4) the mucous coagulates forming an adhesion with the skin and the egg capsules; 5) depression of the spongy corium layer of the dermis and folding of the epithelial layers results in the cavities that contain individual eggs. This scenario is comparable to the observed be-

havior and histological changes in *G. riobambae* and accounts for the “spinulets” of mucous observed in *Stefania* by Rivero (1970); these are simply coagulated strands of mucous in the ducts of the glands. Nonetheless, this hypothesized reproductive behavior has to be verified in *Stefania*.

The developing embryos of all egg-brooding hylids are partly or completely covered by one or two pairs of branchial gills (del Pino and Escobar, 1981). All known embryos of *Stefania* have two pairs of large gills originating from the first and second branchial arches; each gill has a stalk containing an efferent and afferent vessel.

Embryos in different stages of development provide some information on the sequence of development in *Stefania*. Embryos associated with the holotype of *S. ginesi* (FMNH 74041) have four well-developed limbs, which are beyond the foot-plate stage (stage 37 of Gosner, 1960). The second finger is distinctly longer than the first; a tail stub is present. The hind limbs and tail are folded under the belly and are directed anteriorly (Fig. 4). The forelimbs are folded along the flanks and under the chin. The mouth is situated anteroventrally and surrounded by a single row of papillae. In the

position of the keratinized beaks of most hyloid tadpoles, there are small tubercles, a pigmented upper one and a smaller unpigmented lower one. These embryos still have a large amount of yolk.

Embryos associated with the holotype of *S. goini* (AMNH 23193) have completely developed limbs; the first finger is longer than the second. The feet are folded against the ventral body wall, and the tail is absent (Fig. 5). The mouth is wide with serrated edges along the entire length in some but only laterally in others. Apparently these serrations represent the remainder of the papillae of embryos, as seen in those of *S. ginesi*. In the middle of the upper jaw is a small, triangular, keratinized tubercle, presumably the remains of the upper beak. The anterior parts of the anterior pair of gills are pale brown; the rest of the gills are white, thereby giving the embryo as wrapped in its gills a brown and white pole. The color pattern of faint, pale interorbital and dorsolateral stripes and dark dorsal spots is evident.

In the embryos of *S. goini* the gill stalks of both anterior and posterior pairs of gills emerge from a common origin in front of and above the insertion of the forelimbs. The anterior gills are largest and cover the dorsal, anterior, and anteroventral surfaces of the embryo, whereas the smaller posterior pair of gills cover the posterior and posteroventral surfaces of the embryo. The anterior pair of gills is connected across the chest, just anterior to the insertion of the forelimbs, by a transverse membrane. In smaller embryos the gills meet each other but do not

overlap; in larger embryos the gills to do meet across the snout and dorsal part of the head. In one embryo there is simply a narrow gap in the gills on top of the head (Fig. 6). These observations lead us to speculate that once the gills form they do not grow, and as the embryo reaches its full size the gills no longer cover the entire embryo. Our observations on the nature of the gills in *S. ginesi* and *S. goini* are in agreement with Boulenger's (1904) statement that the eggs on the back of the holotype of *S. evansi* contained "tailed larvae with rudimentary organs" and Noble's (1927:93 and 1931:61) illustrations of an embryo of *S. evansi*.

The reproductive mode and parental care exhibited by *Stefania* are one of the most specialized among the anura. Frogs that have direct development of large eggs have a low number of eggs per clutch (Salthe and Duellman, 1973), and prolonged parental care by females tends to be associated with further reduction in clutch size and frequency of breeding (McDiarmid, 1978; Wells, 1981).

The eggs of *Stefania* are large (8-9 mm) and few in number. Boulenger (1904) and Lang (1924) reported 22 and 24 eggs on brooding females of *S. evansi* from Guyana, whereas Rivero (1970) noted 12 on a female of *S. evansi* from Venezuela; KU 167239 from Venezuela was brooding 11 eggs. One female of *S. goini* was brooding 14 eggs. One of *S. ginesi* was brooding eight eggs and another contained eight large ovarian eggs. The holotype of *S. woodleyi* contained five large ovarian eggs when examined by Hoogmoed in 1977, but examination of the abdominal cavity showed that another egg had been present; presumably that egg was lost or removed during prior dissection. When the specimen was re-examined by Hoogmoed in 1980, only three eggs were present. The holotype of *S. roraimae* collected in October contained small ovarian eggs and was not in breeding condition.

The duration of development and egg-brooding is unknown, but it probably requires at least two or three months, as noted for species of *Gastrotheca* having direct development (Duellman and Maness, 1980). Most females having large ovarian eggs or brooding eggs have been collected only in

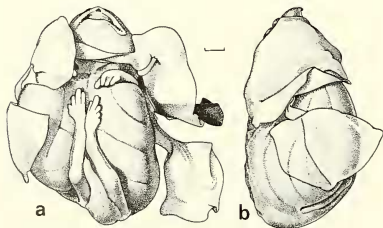


FIG. 4.—Embryo of *Stefania ginesi* (FMNH 74041). a. Ventral view. b. Lateral view. Line = 1 mm. Note tail and papillae at lateral border of mouth.

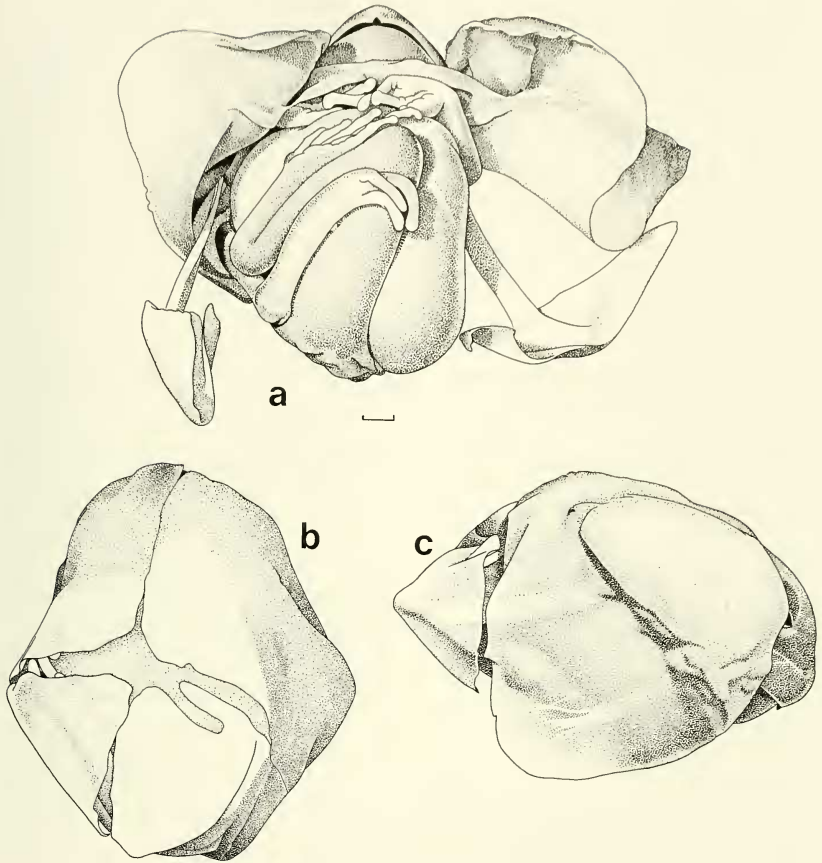


FIG. 5.—Embryo of *Stefania goini* (AMNH 23193). a. Ventral view. b. Dorsal view. c. Lateral view. Line = 1mm. Note individual stalks to each of four gills.

the rainy season (March-August), thereby suggesting that reproduction is restricted to the wetter times of the year. However, a female of *S. woodleyi* containing large ovarian eggs was obtained on 17 August 1957, at the end of the rainy season. If that female had brooded her eggs, she would have been carrying them into the dry season.

Unlike embryos that develop in maternal pouches, such as in *Flectonotus* and *Gastrotheca*, in which there is a gaseous exchange between the maternal lining of the pouch and the gills of the embryo (del Pino

et al., 1975), embryos of *Stefania* probably have no gaseous exchange with maternal tissues, because of the pad of coagulated mucous separating the egg from (but adhering the egg to) the skin of the mother. Thus, respiration must be aerial with all gas exchange occurring between the gills and air across the thin egg capsules. Such respiration requires constantly high atmospheric humidity and would seem to preclude successful development during the dry season, unless the brooding female restricted her activities to localized areas of high humidity.

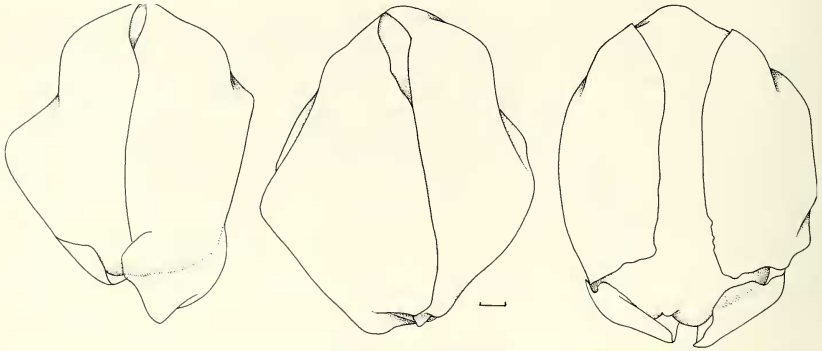


FIG. 6.—Embryos of *Stefania goini* (AMNH 23193) showing from left to right advancing stages of disclosure of the gills covering the embryos. Dorsal views with snout at top. Line = 1 mm.

such as in the spray zone of a waterfall. This may have been true for the brooding female of *S. goini* collected at a waterfall in January. One brooding female of *S. evansi* was observed by day under a rock near a stream in rainy weather in March (Rivero, 1970). Another (KU 167239) was found on a low bush on a rainy night in July.

The only information about possible calls in this genus comes from R. W. McDiarmid's field notes and a statement by Rivero (1970). One male of *S. goini* was found in a crevice by day; a call consisting of five or six notes repeated at intervals of about 10 min led McDiarmid to the site, but the frog was not observed to call. In the description of *S. scalae* (= *evansi*), Rivero (1970:462) stated: "The voice was heard and recorded, but it was accidentally erased afterwards. It consists of a 'whit, whit' sound emitted at infrequent intervals." We have never associated any calling with *S. evansi*. The absence of vocal slits in *Stefania* obviously does not preclude calling by males, but their absence may be indicative that vocalization is uncommon.

KEY TO THE SPECIES

1. Head distinctly wider than long; frontoparietal ridges distinct 2
- Head as wide as long or longer than wide; frontoparietal ridges distinct or absent. 3
2. Toes with basal web; discs on fingers and toes relatively small, covering two-thirds of tympanum; legs short; canthus rostralis indistinct, rounded *S. ginesi*
- Toes one-third webbed; discs on fingers and toes relatively large, covering entire tympanum, legs extremely long; canthus rostralis distinct, angular. *S. goini*
3. Webbing on foot extending to discs of most toes; adults attaining snout-vent lengths of 96 mm *S. evansi*
- Webbing on foot basal; adults attaining snout-vent lengths of no more than 61 mm. 4
4. Skin on dorsum smooth; fingers forming two well-defined groups; first finger distinctly longer (by more than one phalange) than second; dorsum boldly patterned with pale interorbital bar and dorsolateral stripes 5
- Skin on dorsum granular or shagreened; fingers not forming two well-separated groups; first finger only slightly longer (by length of disc) than second; dorsum not boldly patterned. 6
5. Post-tympanic area with large, conical warts; tympanum half diameter of eye; discs on fingers covering half of tympanum; margin of upper eyelid scalloped, bearing small, triangular appendage. *S. marahuauquensis*
- Post-tympanic area with rounded, flat warts; tympanum less than half diameter of eye; discs on fingers covering two-thirds of tympanum, margin of upper

- eyelid smooth, lacking triangular appendage *S. roraimae*
6. Skin on dorsum coarsely granular; tympanum less than half diameter of eye; largest discs on fingers covering one-fourth to one-third of tympanum.
 *S. woodleyi*
- Skin on dorsum shagreened; tympanum more than half diameter of eye; largest discs on fingers covering half of tympanum. *S. riae*

ACCOUNTS OF SPECIES

In the following accounts we present synonymies, diagnoses, and descriptions of each of the species, together with a summary of information on habitat and a statement of distribution. Measurements and proportions for all species are grouped (Table 1), and all information pertaining to their reproductive biology is synthesized in a preceding section.

Stefania evansi Boulenger

Hyla evansi Boulenger, 1904:106 [Holotype—BMNH 1947.2.13.11 from Groete Creek, Essequibo District, Guyana]; Standfuss, 1905:30; Boulenger, 1910:168; Noble 1917:807; Beebe, 1919:208; Nieden, 1923:309; Lang, 1923:410; 1924:478; Crawford, 1931:34; Parker, 1935:527; Fuhn, 1960:59.

Cryptobatrachus evansi—Ruthven, 1922:56; Noble, 1927:93, 1931:60, 61; Fuhn, 1960:59; Goin, 1961:8; Rivero, 1968:140; Porter, 1972:53.

Hyloscirtus evansi—Noble, 1925:9.

"*Hyla*" *evansi*—Noble, 1927:95.

Stefania evansi—Rivero, 1968:143; 1970:466, 467; Hoogmoed in Warren, 1973:79, 86. Gorham, 1974:112; Lescure, 1975:78, 1977:61; Duellman, 1977:181; Hoogmoed, 1979:253, 256, 272.

Stefania scalae Rivero, 1970:456 [Holotype.—MCZ 64373 from La Escalera, road between El Dorado and Santa Elena de Uairén, Estado Bolívar, Venezuela]; Lescure, 1975:78, 1977:61; Duellman, 1977:182; Lamotte and Lescure, 1977:276; del Pino, 1977:22, 24; del Pino and Humphries, 1978:201, 208; Hoogmoed, 1979:272; del Pino, 1980:11, 16. New Synonymy.

Diagnosis.—A very large *Stefania*, females attaining a snout-vent length of 96 mm, males of 53 mm; head longer than wide; frontoparietal ridges absent in specimens from higher elevations, present in those from lowlands; canthus rostralis distinct, angular, straight to shallowly sigmoid; tympanum less than half diameter of eye; first finger distinctly longer than second, discs well developed on all fingers and toes; toes extensively webbed; dorsal skin sha-

TABLE 1.—Measurements and proportions of species of *Stefania*. (Means in parentheses below ranges).

| Species | N-Sex | Snout-vent length (SVL) | Tibia length/SVL | Head length/SVL | Head length/head width | Tympanum/eye |
|--------------------------|-------|-------------------------|---------------------|---------------------|------------------------|-------------------|
| <i>S. evansi</i> | 14 ♂♂ | 39-53 (45.8) | .549-.690 (.603) | .367-.423 (.389) | 1.06-1.23 (1.12) | .35-.48 (.420) |
| | 18 ♀♀ | 37-96 (63.9) | .569-.666 (.623) | .354-.416 (.386) | 1.00-1.20 (1.09) | .36-.60 (.443) |
| <i>S. ginesi</i> | 3 ♂♂ | 46-57 (52.3) | .511-.577 (.550) | .370-.388 (.378) | — (0.90) | .64-.73 (.695) |
| | 2 ♀♀ | 59-63 (61.0) | .492-.552 (.523) | .351-.357 (.354) | — (0.90) | .55-.68 (.613) |
| <i>S. goini</i> | 1 ♀♀ | 93 | .635 | .374 | 0.90 | .64 |
| <i>S. marahuaquensis</i> | 1 ♂♂ | 36 | .586 | .391 | 1.10 | .48 |
| <i>S. riae</i> | 2 ♂♂ | 55-56 (55.5) | .588-.609 (.600) | .360-.373 (.367) | 1.00-1.03 (1.02) | .54-.62 (.580) |
| | 1 ♀♀ | 59 | .586 | .369 | 1.00 | .60 |
| <i>S. roraimae</i> | 1 ♀♀ | 46 | .628 | .372 | 1.03 | .44 |
| <i>S. woodleyi</i> | 1 ♀♀ | 61 | .563 | .397 | 1.07 | .48 |

greened, uniformly brown, with a pattern of dark chevrons, or with a bold pattern of narrow pale interorbital bar and dorsolateral stripes; black canthal and supratympanic stripes and row of black spots on the anterior surface of thigh near knee; belly dull white, throat and chest with or without angular brown spots.

Description.—Head longer than wide, as wide as adjacent part of body; depth distinctly less than half length. Snout pointed in dorsal view, rounded to truncate in profile, distinctly longer than horizontal diameter of eye. Distance between eye and nostril slightly shorter than, or equal to, horizontal diameter of eye, more than twice distance between nostril and tip of snout. Canthus rostralis distinct, angular, straight to shallowly sigmoid; upper part of loreal region vertical, lower part sloping gradually to unflared lip, resulting in extremely concave loreal region. Nostrils small, round, directed laterally and posterodorsally in slightly elevated areas just below canthus rostralis (Fig. 7). Distance between nostrils 59–90% of interorbital distance in females, 69–92% in males, 1.1–1.5 times distance between nostril and tip of snout; area between nostrils flat to slightly concave. Interorbital space flat to slightly concave, in most females distinctly wider than an upper eyelid, in most males distinctly narrower. Texture of upper eyelid like rest of dorsum. Frontoparietal ridges present in large lowland specimens, absent in specimens from higher elevations. Temporal region nearly vertical. Tympanum distinct, surrounded by a bony annulus, large, round, distinctly to slightly less (35–50%) than half the horizontal diameter of eye, separated from eye by a distance distinctly less than its diameter, except in large females (more than diameter of tympanum). Supratympanic fold distinct, slightly curved, extending from posterior corner of eye to just above insertion of forelimb, obscuring upper edge of tympanum, with or without an indistinct dorsolateral continuation.

Choanae large, oval to oblongly triangular. Prevomerine processes large, transverse, between choanae, each bearing 4–12 (mostly 7–10) teeth. Lower numbers generally in juveniles. Tongue large, round. Pupil

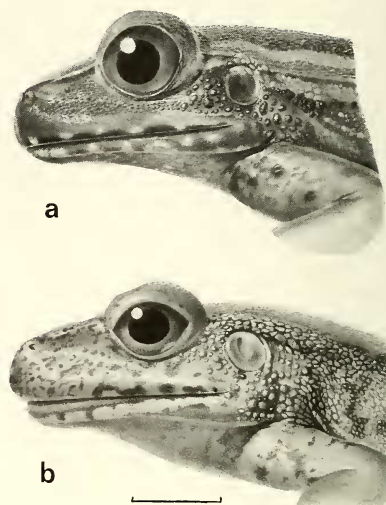


FIG. 7.—Lateral views of heads of *Stefania evansi*: a. RMNH 19458, ♀. b. BMNH 1947.2.13.11 (holotype). Line = 10 mm.

horizontally oval. Palpebral membrane not reticulated, with a brown pigmented zone along its upper rim.

Skin of dorsum, flanks, and dorsal parts of limbs shagreened. Loreal region granular with some projecting larger pustules. Temporal region and area ventral and posteroventral to tympanum with rounded warts, Belly, anterior part of flanks and posteroventral part of thighs moderately granular. Throat and ventral parts of rest of limbs smooth. Anal opening directed posteroventrally at midlevel of thighs, with short, transverse anal sheath.

Pollical tubercle large, distinct, oval; palmar tubercle large, distinct, bifid. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles on palm and base of fingers, round, variable in size, flat. First finger distinctly longer than second, shorter than fourth, third longest. Fusion of third and fourth finger at their base not very distinct. Fingers completely devoid of webbing. Discs on fingers large, transversely oval, wider than penultimate phalange, smallest on first, largest on third and fourth fingers. Largest discs nearly com-

pletely covering the tympanum. Males with pale brown nuptial pad covering dorsal and medial surface of the first phalange of first finger. Nuptial pad on dorsal surface extending from articulation with second phalanx halfway down the first phalanx, on medial surface covering entire length of first phalanx, from dorsal surface of pollical tubercle to articulation with second phalanx (Fig. 8).

Inner metatarsal tubercle protruding, large, distinct, oval; outer metatarsal tubercle flat, small, indistinct, round. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles present on base of toes, indistinct, flat, small, round. Third toe slightly shorter than fifth. Toes extensively webbed, slightly more so in females than in males, webbing formula I1-(1-1/2)II1-2 III1-(2-3)IV(2-2 3/4)-1V. Discs on toes large, oval, largest one as large as or only slightly smaller than largest ones on fingers, distinctly wider than penultimate phalanx. When hindlimbs folded and flexed at right angles to sagittal plane of body, heels overlapping considerably.

There are three distinct patterns, which in life are colored as follows: Morph A has a pale brown back without pattern, flanks



FIG. 8.—Foot (a) and hand (b) of *Stefania evansi*, RMNH 18022. ♀. Line = 1 mm.

yellowish white, posterior part of belly and ventral surface of thighs yellow, throat and chest white. The other morph (B) has a dark brown back with ochre-yellow interorbital and dorsolateral stripes, sometimes with an intricate extension of the interorbital bar on the snout; upper lip orange; upper part of flank red to reddish brown, remainder of flank brown; tympanum chestnut-brown. Upper part of iris gold-colored, lower part dark red-brown; throat and chest dark brown with white spots, belly pale brown with dark brown spots; ventral surface of hind limbs dark brown (field data, MSH and WED).

Rivero (1970:460) described living specimens from the La Escalera region as greenish gray to greenish brown with or without dark brown mottling, upper lip with oblique yellowish line, posterior half of belly yellow, lower flanks yellow or marbled with yellow, throat and chest white to dirty white, ventral surfaces of hind limbs yellowish brown to yellow marbled with brown, webs purplish gray to purplish brown.

Mr. A. N. Warren provided MSH with slides of BMNH 1970.583 while still alive and from them the following description was made (morph C): dorsum yellowish brown with reddish brown chevrons, bordered by black; transverse bars on limbs reddish brown. Area in front of and behind tympanum reddish, upper lip white with black bars. Lower part of flanks, belly, and chest white. Iris golden brown. RMNH 19450, showing faint traces of chevrons, in life had a pale brown dorsum; the posterior part of belly and ventral surface of thighs were yellow. The throat and chest were white and the flanks yellowish white.

In preservative the three pattern-morphs also can be distinguished. A.—A plain morph with a uniformly colored dorsum, with traces of a paler dorsolateral band. B.—A striped morph with distinct pale, narrow interorbital and dorsolateral lines forming a triangular figure. C.—A patterned morph with dark chevrons on the back (Fig. 9).

Morph A.—The dorsum is pale brown to pale gray, with or without dark brown mottling. A black canthal stripe may be present. A distinct black supratympanic stripe increases in width posteriorly and reaches the anterior part of the flanks; in some speci-

mens there are isolated black spots on the flanks. The snout is paler than the rest of the dorsum; a vertical pale stripe is present on the tip of the snout. Other details of coloration are the same as Morph B. This morph is known from both the lowlands of Guyana ("*Stefania evansi*"), where it is relatively common, and from the La Escalera region ("*Stefania scalae*"), where it is relatively rare.

Morph B.—The dorsum is dark brown with a pale brown to whitish interorbital stripe, connected on the eyelids by a pair of dorsolateral stripes that meet above the vent, therefore forming a triangle having its apex above the vent and its base between the eyes. On the snout of many specimens there is an intricate pattern of pale lines, connected with the interorbital line, and dark brown spots forming a T-shaped mark. A pale vertical stripe is present on the tip of the snout. A black supratympanic stripe is present, but it is not as conspicuous as in Morph A. On the upper part of the flanks there are dark brown spots below the dorsolateral line; the rest of the flanks are marbled brown and gray. Dark brown transverse bars are present on the limbs; these are especially distinct on the dorsal surfaces of the thigh and shank. The anterior parts of the bars on the thigh are solid black, thus forming a row of the black spots on the anterior surface of the thigh, especially distally. The posterior

surfaces of the thighs are brown, marbled with cream. The upper lip is black with white spots, most distinct posteriorly. The lower lip is brown with small white spots. The tympanum is chestnut-brown. The throat and chest are brown, marbled with white and having a longitudinal, median white stripe; in some specimens the throat and chest are white with a few gray or brown spots. The belly is white to cream with or without angular brown spots. The ventral surfaces of the limbs are brown or white marbled with brown. This morph is known from many specimens from the La Escalera region ("*Stefania scalae*"), where it is the most common morph, and from one specimen (UMMZ 85175) from Membaro Creek, Guyana, in which the pattern is discernible but not distinct.

Morph C.—The dorsum is pale to dark brown with a large, dark brown interorbital spot, two triangular spots on the scapular region (one on each side of the vertebral column with their apices pointing towards it), and five chevrons across the vertebral column. Distinct transverse bars are present on the limbs. Black canthal and supratympanic stripes are present. A series of dark brown spots is present on the flanks. Otherwise the coloration is the same as in Morph B. This pattern is most often found in specimens from the lowlands of Guyana (BMNH 1947.2.13.11, BMNH 1970.538,

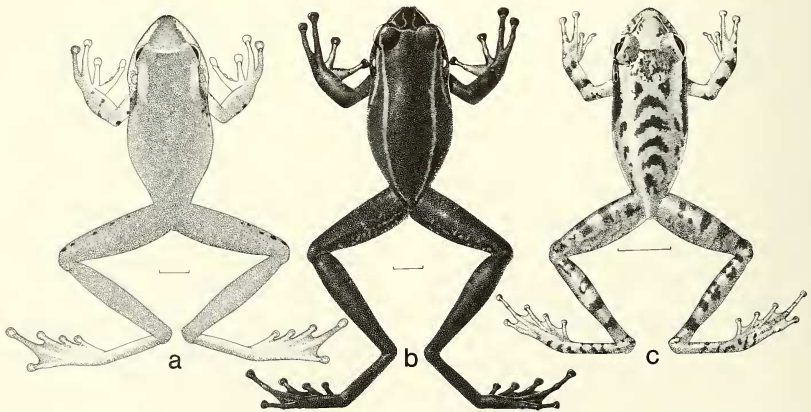


FIG. 9.—Color morphs of *Stefania evansi*: a. Plain morph (RMNH 18022, ♀). b. Striped morph (RMNH 19458, ♀). c. Patterned morph (OUM 13501, ♀). Lines = 10 mm.

UMMZ 85174, OUM 13501), but also in a single specimen (RMNH 19450) from La Escalera. The pattern is very faint in the latter specimen. The pattern seems to be best developed in juveniles (OUM 13501); with increasing age the brown chevrons tend to disintegrate into numerous small spots, thus obscuring the original pattern (BMNH 1947. 2.13.11). One specimen (OUM 13501) has green bones.

Habitat.—Many of the frogs collected recently have brief habitat notes on the labels; from these it is clear that this species in Guyana (field notes A. N. Warren and J. D. Woodley) inhabits primary forest along creeks. Specimens were found on the banks of rocky creeks, on branches overhanging these creeks, and on rocks in or along creeks. Specimens were found in the same general habitat in La Escalera region, Venezuela—along fast-flowing creeks in montane forests, at night sitting on branches and on sandstone rocks (field observations WED, 1974, and MSH, 1978), under rocks by day (Rivero, 1970:462), or on vegetation by day (field observation MSH, 1978). All specimens have been found on the ground or within 50 cm above it. Most climbing is on boulders.

Distribution.—*Stefania evansi* as here recognized is known from Kartabo and Groete Creek, Guyana, westward to La Escalera, Venezuela (Figs. 2, 10). The species occurs at elevations of 10–1402 m (Hoogmoed, 1979:272) and occurs in tropical rainforests in Guyana near the Essequibo River and montane rainforests at elevations of 1371 m (Warren, 1973:80) on Mount Roraima.

Remarks.—On the basis of the extensive series of specimens from Guyana, commonly referred to *Stefania evansi*, and from the La Escalera region in Venezuela, until now referred to as *S. scalae*, we conclude that only one species is recognizable. The earliest name for these frogs is *Stefania evansi* (Boulenger). *Stefania scalae* was described on the basis of six specimens, which were said to differ from *S. evansi* in the webbing of the feet (slightly less webbed in *S. scalae* than in *S. evansi*) and in the size of the tympanum relative to the eye (half the diameter of the eye in *S. scalae*, three-

fourths in *S. evansi*). The data assembled by us from much more material than was available to Rivero (1970) show that neither of these characters holds true and that there is considerable overlap in these characters in specimens from Guyana and Venezuela. There seems to be continuous variation encompassing both *S. evansi* and *S. scalae*. Specimens from La Escalera region ("*Stefania scalae*") tend to be smaller (SVL: 19 ♂♂ 36.8–50.0, \bar{x} = 42.3, SD = 6.49; 10 ♀♀ 58.6–17.0, \bar{x} = 63.6, SD = 5.19), have slightly less webbed toes, have fewer eggs (11 or 12 versus 22 or 24) on the back, lack frontoparietal ridges, and have the zygomatic ramus of the squamosal reaching only halfway to the maxilla. Specimens from Guyana ("*Stefania evansi*") tend to be larger (SVL: 7 ♂♂ 64.0–89.0, \bar{x} = 72.3, SD = 8.62), have more fully webbed toes, have more eggs (22 or 24 versus 11 or 12) on the back, have frontoparietal ridges, and have the zygomatic ramus of the squamosal reaching to the maxilla. The latter three characters probably are directly related to body size; larger individuals have more ossified skulls resulting in exostosis. There-

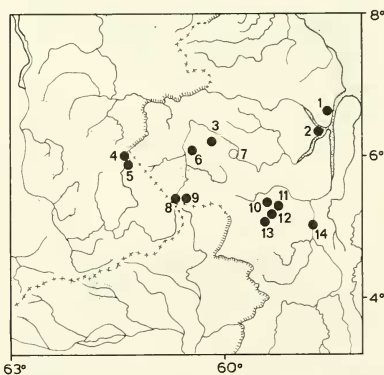


FIG. 10.—Known distribution of *Stefania evansi* in Guyana and eastern Venezuela: 1. Groete Creek; 2. Kartabo; 3. Makreba Falls, Kurupung River; 4. La Escalera, Km 112; 5. La Escalera, Km 125; 6. Membaro Creek (= Membaru River); 7. Literature record (Noble, 1927); 8. Mount Roraima; 9. Pipillipai; 10. Mount Kanaima (= Kaneima); 11. Amatuk Falls, Potaro River; 12. Echerak; 13. Karisparu; 14. Haiowa Falls, Essequibo River. Grenada Island could not be located on any map; probably it is in the Mazaruni River near Kartabo.

fore, the characters differentiating *S. evansi* and *S. scalae* show continuous variation from La Escalera to lowland Guyana; in the absence of any evidence of genetic isolation between the extreme populations, we do not consider the differences to be sufficiently important to warrant the recognition of two species.

Stefania ginesi Rivero

Cryptobatrachus sp. Ginés, 1959:123.

Stefania ginesi Rivero, 1968:145 [Holotype.—FMNH 74041 from Chimantá-tepui, Estado Bolívar, Venezuela], 1970:466, 467, 471-473; Gorham, 1974:112; Lescure, 1975:78, 1977:61; Duellman, 1977:181; Hoogmoed, 1979:272.

Stefania sp. "C" Hoogmoed, 1979:272.

Diagnosis.—A large *Stefania*, females attaining a snout-vent length of 63 mm, males of 57 mm; head distinctly wider than long; frontoparietal ridges distinct; canthus rostralis indistinct, rounded, concave; tympanum in adults two-thirds diameter of eye, in smallest juvenile half diameter; first finger only slightly longer than second, discs on fingers and toes small; toes webbed basally; legs short; skin on dorsum, flanks, top and side of head strongly tubercular; dorsum in adults dark brown or gray with irregular pattern, with or without pale interorbital bar and dorsolateral lines; juveniles grayish green with indistinct darker chevrons; flanks marked with gray and white spots; limbs pale with darker transverse bars; throat and belly creamish to pale gray with darker spots.

Description.—Head wider than long, distinctly wider than adjacent part of body, depth distinctly less than half the length. Snout ovoid in dorsal view, truncate to sloping in profile, short, only slightly longer than the horizontal diameter of the eye. Distance between eye and nostril distinctly shorter than horizontal diameter of eye, more than twice the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, concave, with rounded tubercles; loreal region concave, gradually sloping to upper lips. Lips not flared. Nostrils small, round, in slightly elevated areas just below canthus rostralis, directed laterally and slightly dorsally. Distance between nostrils

half interorbital distance in adults, two-thirds in juveniles, 1.3 times distance between nostril and tip of snout; area between nostrils slightly concave. Interorbital space concave, accentuated by strongly developed frontoparietal ridges, as wide as, or wider than, upper eyelid. Upper eyelid tubercular. Temporal region sloping gradually. Tympanum distinct, surrounded by a bony annulus; large, round, half to two-thirds the horizontal diameter of eye; separated from eye by distance less than its diameter. Supratympanic fold indistinct, straight, horizontal, warty, extending from posterior corner of eye to just posterior to tympanum, obscuring the upper edge of tympanum (Fig. 11).

Choanae large, oval. Prevoemerine processes large, positioned transversely between choanae, bearing two short, straight rows of 2-6 teeth each. Teeth in USNM 212042 extremely long. Tongue large, round. Pupil horizontally oval. Palpebral membrane not reticulated, but with a brown pigmented zone along its upper rim.

Skin on dorsum, top and sides of head, and flanks strongly tubercular. Temporal and post-tympanic region covered with large, round, flat tubercles. Loreal region with smaller and less numerous, flat tubercles. A row of three elevated tubercles, increasing in size posteriorly, on canthus rostralis. Skin on limbs smooth or covered with small pustules. Skin on throat smooth, on belly coarsely granular. Ventral surface of limbs smooth. Anal opening directed posteroventrally at midlevel of thighs, with short, transverse anal sheath.

Pollical tubercle large, distinct, oval; palmar tubercle large, distinct, bifid. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles on palms and base of fingers, distinct, round, flat. First finger slightly longer than second, shorter than fourth; third longest. First and second fingers apparently forming an operational unit that is opposable against third and fourth fingers, which are fused at their base. Fingers completely devoid of web. Discs on fingers large, round (first finger) to oval (other fingers), distinctly wider than penultimate phalanx, largest on third and fourth fingers (approximately covering two-thirds

of tympanum). In juveniles, discs cover about half of tympanum (Fig. 12).

Inner metatarsal tubercle large, distinct,

oval; outer metatarsal tubercle small, indistinct, round. Subarticular tubercles large, distinct, single, round. Supernumerary tu-

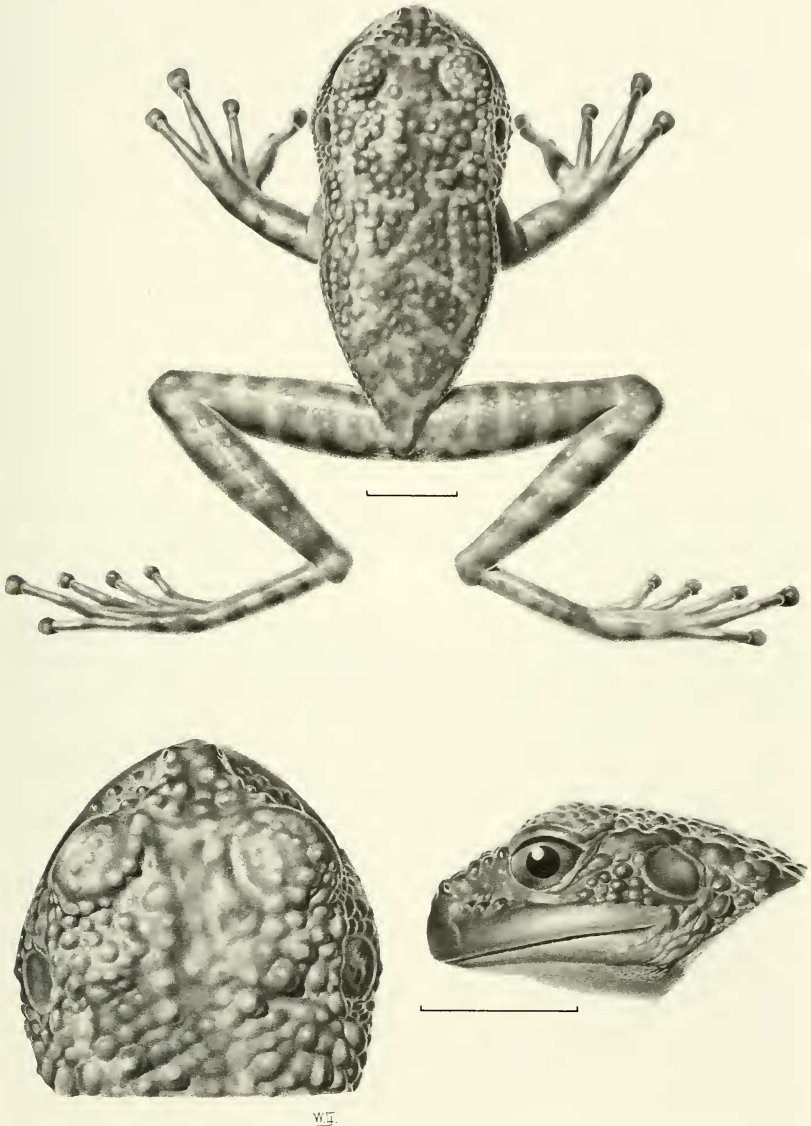


FIG. 11.—*Stefania ginesi*, USNM 212040, ♂. Lines = 10 mm.

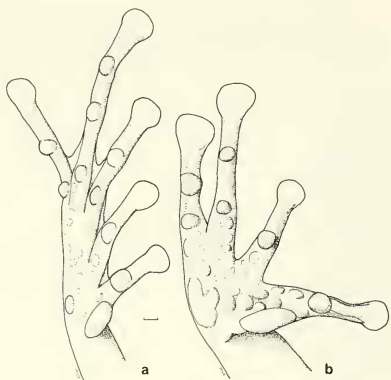


FIG. 12.—Foot (a) and hand (b) of *Stefania ginesi*, USNM 212040, ♂. Line = 1 mm.

bercles on sole and base of toes small, indistinct, round. Third toe slightly shorter than fifth. Webbing formula: $12-(2^{1/2}-2^{3/4})$ II $(1^{3/4}-2)-3$ III $2-(3^{1/2}-3^{2/3})$ IV $(3^{1/3}-3^{1/2})-2$ V. Discs on toes moderately large, but smaller than those on fingers, oval, distinctly wider than penultimate phalanx. When hind limbs folded and flexed at right angles to sagittal plane of body, heels overlap considerably.

The color in life of two juveniles (BMNH 1975.1361-62) was described by the collector, A. N. Warren, as "small, dark . . . with gold speckles." The color in life of USNM 212040 was described as "dorsum mottled brassy brown, dark brown and opalescent white; limbs barred; rump patch purplish; ventrally greenish gray; iris silver gray with black reticulations" (Fig. 13). The skin was described as very warty. USNM 212044 in life was "mottled dark & lighter brown on back, blue gray in axilla & groin; some brassy color on back & legs; pupil horizontal; chin dirty greenish white" (both citations from R. W. McDiarmid's field notes).

In preservative the back is dark brown to gray with usually indistinct, irregular paler markings, among which a transverse inter-orbital bar and dorsolateral lines can be discerned (Figs. 11, 14). There are more or less distinct, narrow, transverse black bands on the dorsal surfaces of thighs, shanks, feet and forearms. The venter is brownish white to gray, with irregularly dispersed angular brown spots, most numerous on throat and chest. Juveniles are greenish gray with small, white spots and brown markings, of which several chevron-shaped marks are

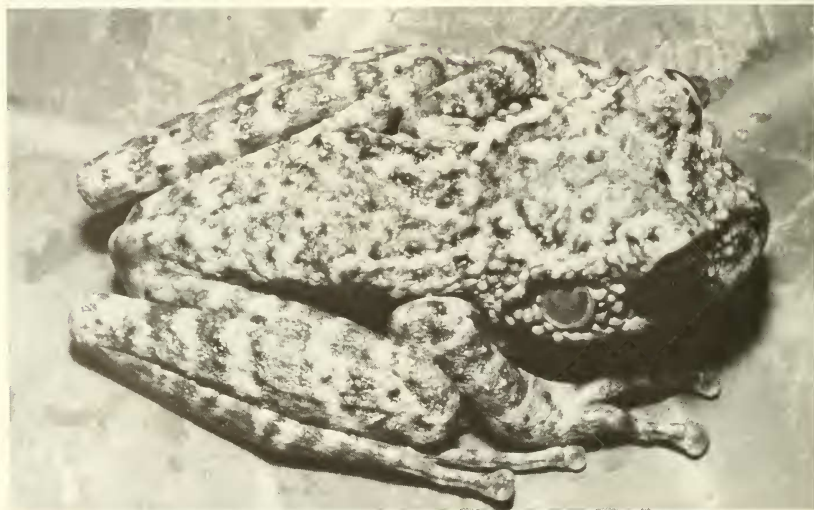


FIG. 13.—*Stefania ginesi*, USNM 212040, ♂; photographed in life by R. W. McDiarmid.

recognizable on the posterior part of the back. Indistinct brown interorbital bar and canthal stripes are present. The limbs have distinct, narrow, brown transverse bars on the dorsal surfaces (5-6 on thigh). The posterior surface of the thighs are brown with greenish gray spots that are continuations of the dorsal bars. The fingers and toes are pale with dark cross bars. To the naked eye, the venter is immaculate greenish white, but under magnification, numerous melanophores tend to be arranged in clusters with small unpigmented areas between them.

Habitat.—The holotype was collected at an elevation of 2225 m on “rock outcrops near E. branch of head water Río Tirica” (Rivero, 1968:145). The two juveniles from Auyán-tepui (BMNH 1975.1361-62) were caught “under wet bare rocks near small temporary pools at an elevation of 2,400 meters, close to the cliff edge and to the bust of the Liberator” (A. N. Warren’s field notes). USNM 212040 was “found in a deep

crack amongst large sandstone boulders” (McDiarmid’s field notes) on the top of Eruoda-tepui at an elevation of 2300 meters. Three specimens (USNM 212041-43) were in bromeliads, *Brocchinia hechtioides*, “growing at the edge of the water,” in an open area on top of Torona-tepui at an elevation of 2450 meters, and USNM 212044 was at the edge of a pond surrounded by *Sphagnum*. These specimens (USNM) all were obtained by day. From these data it seems that this species is an inhabitant of wet, rocky places, without any forest growth around, on the summits of sandstone tepuis.

Distribution.—Thus far *Stefania ginesi* is only known from five tepuis, all in a restricted area in eastern Venezuela (Figs. 2, 15). Eruoda-tepui and Torona-tepui are on the eastern edge of Acopán-tepui, which is part of the large complex of tablelands collectively known as Chimantá-tepui. Aprada-tepui is northwest of Chimantá-tepui and south of Auyán-tepui. The known al-

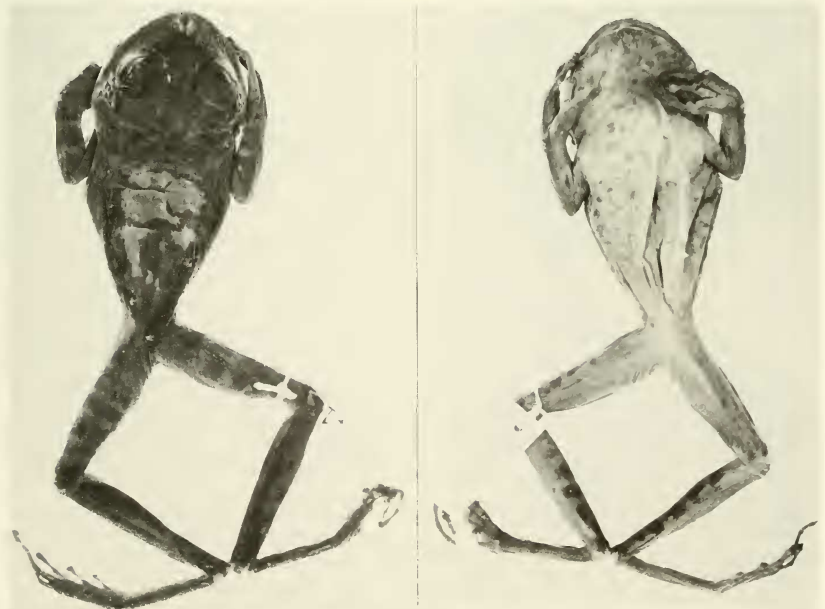


FIG. 14.—Dorsal and ventral views of the holotype of *Stefania ginesi*, FMNH 74041, ♀. Note impressions of eggs on dorsum.

itudinal distribution of this species is 2225–2450 m.

Remarks.—Although this species was only described in 1968, it had been completely depicted nine years earlier by Ginés (1959:123-4), who reported having examined a specimen of *Cryptobatrachus* belonging to the Chicago Museum of Natural History and coming from Chimantá-tepui. The specimen was figured. On the basis of the figures and the data published by Ginés (1959) it is clear that this specimen was the same as the holotype of *Stefania ginesi* Rivero, which was collected on 12 February 1955 (according to data supplied on the loan invoice by the Field Museum of Natural History) and not on 16 January 1965, as stated by Rivero (1968:145) in his description of *Stefania ginesi*. From Ginés' (1959:124) paper it is evident that he intended to publish a complete description of his *Cryptobatrachus* sp., but as far as we can ascertain, no such description ever appeared; thus Rivero's (1968:145, 147) description of this species, which he named in honor of Ginés, was the first to be published.

Stefania goini Rivero

Stefania goini Rivero 1968:145 [Holotype.—AMNH 23193 from Vegas Falls, Cerro Duida, Territorio Amazonas, Ven-

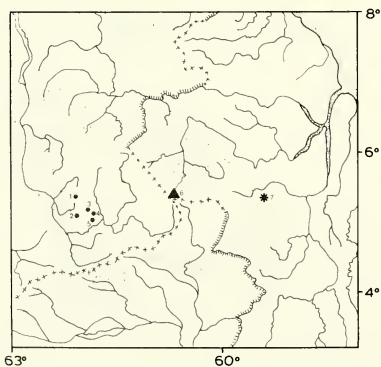


FIG. 15.—Border region of Venezuela, Guyana, and Brasil showing the known localities for *S. ginesi* (dots), *S. roraimae* (triangle), and *S. woodleyi* (asterisk). 1. Auyán-tepui; 2. Aprada-tepui; 3. Chimantá-tepui; 4. Eruoda-tepui; 5. Torona-tepui; 6. Mount Roraima; 7. Mount Kanaima.

ezuela], 1970:466, 468, 471–473; Gorham, 1974:112; Lescure, 1975:78, 1977:61; Duellman, 1977:181; Hoogmoed, 1979:254, 272.

Diagnosis.—A very large *Stefania*; single known adult female having a snout-vent length of 93 mm; head wider than long. Frontoparietal ridges distinct; canthus rostralis distinct, angular, straight. Tympanum nearly two-thirds the diameter of the eye. First finger distinctly longer than the second; discs well developed on all fingers and toes. Feet about one-third webbed; legs extremely long. Skin on dorsum granular, with an indistinct pattern of pale interorbital and dorsolateral lines. Throat with large, angular, dark brown spots; belly immaculate.

Description.—Head wider than long, wider than adjacent part of body, depth half length. Snout rounded in dorsal view, sloping in profile, distinctly longer than horizontal diameter of eye, which equals distance to nostril. Distance between eye and nostril 2.5 times distance between nostril and tip of snout. Canthus rostralis distinct, angular, straight, with large knobs; loreal region distinctly concave, sloping steeply to rounded lips. Nostrils large, round, in swollen areas just below canthus rostralis, directed laterally and posteriodorsally. Distance between nostrils 52% of interorbital distance, equal to distance between nostril and tip of snout; area between nostrils flat. Interorbital space nearly twice width of upper eyelid, distinctly concave because of strongly developed frontoparietal ridges, which continue to back of skull. Temporal region sloping, tympanum directed dorsolaterally. Tympanum distinct, surrounded by bony annulus, large, round, nearly two-thirds (63–65%) horizontal diameter of eye, separated from eye by a distance more than three-quarters its diameter. Supratympanic fold distinct, curved, obscuring upper edge of tympanum.

Choanae wide, elongated slits. Prevomerine processes large, positioned transversely between the choanae, bearing 9–10 teeth each. Tongue large, cordiform. Pupil horizontally oval. Palpebral membrane not reticulated, with a pigmented zone along its upper rim.

Skin of dorsum and flanks finely granular, on top of head (including upper eyelids) and on loreal region with scattered pustules. Temporal region with small round tubercles around tympanum. Belly and posteroventral surfaces of thighs moderately granular. Throat, chest, and dorsal surfaces of limbs finely shagreened, lower surfaces of limbs smooth. Anal opening directed posteroventrally at midlevel of thighs, with indistinct transverse anal sheath.

Pollical tubercle large, oval, projecting; palmar tubercle large, distinct, round, single. Subarticular tubercles large, round, projecting, single. Supernumerary tubercles absent. Length of fingers from shortest to longest: 2-1-4-3. Fusion of third and fourth fingers not very distinct. Fingers completely devoid of webbing. Discs on fingers large, round, twice as wide as penultimate phalange; discs on first finger hardly smaller than those on other fingers. Largest discs present (those on fourth fingers; discs of third fingers missing, due to previous dissection) not completely covering tympanum (Fig. 16).

Inner metatarsal tubercle large, oval, projecting, visible from above; outer metatarsal tubercle small, round, flat. Subarticular tubercles large, round, projecting, single. Supernumerary tubercles indistinct, flat,



FIG. 16.—Hand (a) and foot (b) of *Stefania goini*, AMNH 23193, ♀. Line = 1 mm.

round, few in number. Length of toes from shortest to longest: 1-2-3-5-4. Third toe only slightly shorter than fifth. Toes one-third webbed; Webbing formula: I2-2⁺ III^{1/2}-3-III2-3^{1/4} IV3-2-V. Discs on toes round, large, larger than largest discs on fingers present (discs of third fingers dissected). When hindlimbs folded and flexed at right angles to sagittal plane of body, heels overlap considerably.

Dorsum dark brown with paler mottling, an indistinct pale interorbital stripe connected with faint dorsolateral stripes, visible through the gray mucous layer covering the dorsum from just posterior to the head to just above the anus (Fig. 17). Flanks gray with dark brown spots. Limbs grayish brown with numerous transverse dark brown bands. Throat brownish white with numerous large, angular, dark brown spots; chest with a few spots, and belly immaculate.

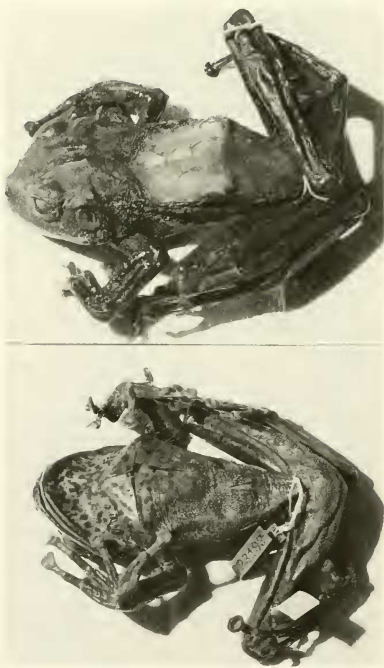


FIG. 17.—Holotype of *Stefania goini*, AMNH 23193, ♂. Note frontoparietal ridges and impressions of eggs on dorsum.

Distal part of ventral surface of thighs with small, brown spots. Bones green.

Habitat.—No data on the habitat of this species are available, but the name of the type locality suggests that the specimen was caught in a rocky area near a fast-flowing creek.

Distribution.—This species is known only from the type locality, Vegas Falls, 1400 m, on Cerro Duida, a large sandstone tepui in southern Venezuela, close to the confluence of the Cassiquiare Canal with the Río Orinoco (Fig. 2).

Remarks.—On the basis of the shape of the head, which is distinctly wider than long and has well-developed frontoparietal ridges, Rivero (1970:465) placed *Stefania goini* and *S. ginesi* together in the *S. goini* group, which differs in head shape and presence of frontoparietal ridges from the other known members of the genus comprising the *S. evansi* group.

Stefania marahuacuensis Rivero

Hyla marahuacuensis Rivero, 1961:118 [Holotype.—MCZ 28566 from Caño Caju, Cerro Marahuaca, Territorio Amazonas, Venezuela], 1965:416, 418, 1968:140, 145.

Stefania marahuacuensis Rivero, 1966:140, 1970:467, 468, 471, 473, 1971:186; Gorham, 1974:100; Lescure, 1975:78, 1977:61; Duellman, 1977:182; Hoogmoed, 1979:254, 256, 272.

Diagnosis.—A small species of *Stefania*, attaining a snout-vent length of 36 mm; head longer than wide. Frontoparietal ridges absent; canthus rostralis distinct, angular, straight. Tympanum approximately half diameter of eye. First finger longer than second; discs on fingers well developed; those on toes only slightly smaller. Feet basally webbed. Skin on back smooth. Upper eyelid with small triangular appendage. Large coneiform warts in post-tympanic and anterior dorsolateral areas. Snout distinctly paler than back, with more or less distinct interorbital bar and dorsolateral stripes; posterior part of dorsum with dark brown spots in three transverse rows, each row consisting of three to four spots, the vertebral ones largest and most distinct.

Description.—Head longer than wide,

distinctly wider than adjacent part of body, depth distinctly less than half length. Snout ovoid in dorsal view, truncate in profile, short, only slightly longer than horizontal diameter of eye. Distance between eye and nostril distinctly shorter than horizontal diameter of eye, more than twice distance between nostril and tip of snout. Canthus rostralis distinct, angular, straight; loreal region strongly concave, gradually sloping to unflared lips. Nostrils large, oval, in protuberant areas directed laterally and posterodorsally just below canthus rostralis. Distance between nostrils two-thirds interorbital distance, 1.3 times distance between nostril and tip of snout; area between nostrils concave. Interorbital space convex, wider than upper eyelid. Upper eyelid rugose, with small but distinct, flat, triangular appendage on posterior edge and a scalloped margin. Frontoparietal ridges absent. Temporal region sloping steeply. Tympanum distinct, surrounded by a bony annulus, large, round, half horizontal diameter of eye; separated from eye by a distance less than its diameter. Supratympanic fold distinct, curved, extending from the posterior corner of the eye to above insertion of forelimb, obscuring upper edge of tympanum; fold flat, indistinct anteriorly, culminating in narrow, elevated, short ridge behind tympanum. Numerous coneiform warts are present posterior to post-tympanic ridge, largest warts above insertion of forelimb, decreasing in size posteriorly, disappearing half way along flanks (Fig. 18). Choanae large, oval. Pre-vomerine processes large, transverse between choanae, bearing short, straight rows of nine teeth each. Tongue large, round. Pupil horizontally oval. Palpebral membrane not reticulated, with a brown pigmented zone along its upper rim.

Skin on dorsum, top of head, throat, and limbs smooth. Skin on belly indistinctly shagreened. Temporal and loreal region smooth. Post-tympanic area with coneiform warts (see above). Flanks, especially anterior part, granular. Anterior part of dorsolateral area with coneiform warts, each wart in a dark brown spot. Anal opening directed posteriorly at upper level of thighs, with short, transverse anal sheath.

Pollical tubercle large, distinct, oval; pal-

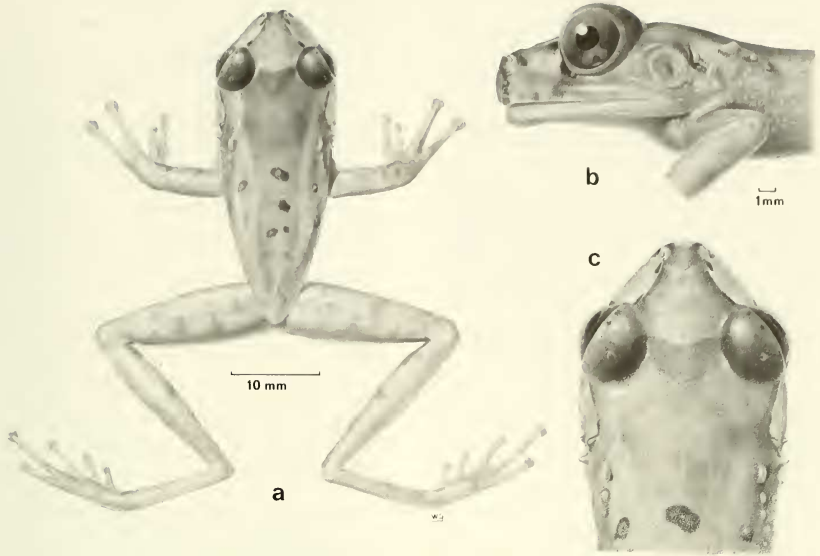


FIG. 18.—*Stefania marahuaguensis*, UPRM 2869, ♂. a. Dorsum. b. Lateral view of head. c. Dorsal view of head and anterior trunk; note conical post-tympanic warts and triangular dermal flap on eyelid.

mar tubercle large, distinct, bifid. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles on palm and base of fingers, distinct, round, flat. First finger longer than second, shorter than fourth, third longest. First and second fingers apparently forming an operational unit that is opposable to third and fourth fingers, which are fused at their base. Fingers completely devoid of web. Discs on fingers large, round (first finger) or oval (other fingers), wider than penultimate phalange, largest on third and fourth fingers (about half of tympanum diameter) (Fig. 19).

Inner metatarsal tubercle large, distinct, oval; outer metatarsal tubercle small, indistinct, round. Subarticular tubercles large, distinct, single, round. A few small, indistinct, flat, supernumerary tubercles. Third toe slightly shorter than fifth. Toes webbed basally. Webbing formula: I2-2¹/₃III³/₄-3III2-3¹/₂IV3¹/₂-2V. Discs on toes well developed, smaller than those on fingers, round to oval, distinctly wider than penultimate phalange. When hind limbs folded and

flexed at right angles to sagittal plane of body, heels overlap considerably.

In life, one specimen (UPRM 2869) was yellowish brown with dark spots; the belly was white (Rivero, 1972:187).

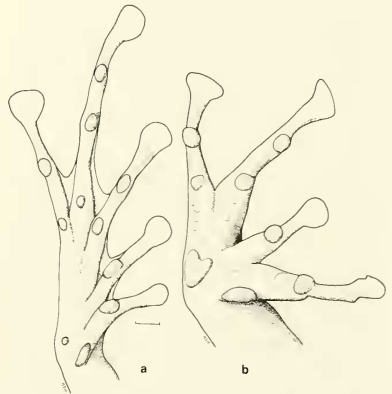


FIG. 19. Foot (a) and hand (b) of *Stefania marahuaguensis*, UPRM 2869, ♀. Line = 1 mm.

In preservative, the mid-dorsum is pale brown, bordered by more or less distinct, narrow, pale dorsolateral stripes, which are connected by a pale interorbital stripe. Posteriorly on the dorsum is a vertebral row of four to five dark brown spots (Fig. 20). These vertebral spots form part of transverse, convex rows of dark brown spots, each consisting of three or four spots, with the lateral ones on the upper part of the flanks lateral to the dorsolateral stripes; each lateral spot encloses a tubercle. The vertebral spots are larger than the lateral spots. The dorsal surface of the snout and loreal region are cream, distinctly paler than the dorsum. Two dark brown spots are present on the canthus rostralis; one is behind the nostril and one just in front of the eye. Dark brown vertical bars are present below the nostril and the eye. An inverted U-shaped, brown mark is present on the upper lip between the bars below the nostril and the eye; the lower parts of these marks are much more distinct than the rest. A dark brown supratympanic stripe is present. The flanks have obliquely arranged brown spots. The upper surfaces of the limbs are pale brown with more or less clearly defined, brown, transverse spots. The posterior surfaces of the thighs are dark brown with cream spots. Three or four well-defined dark brown spots are present on the anterior surfaces of thighs near the knees, leaving a cream zigzag line between them and the spots on the dorsal surfaces. To the naked eye the venter is immaculate cream, but under magnification numerous melanophores tend to be arranged in clusters with small, unpigmented areas between them. A gray band is present on the ventral surface of each toe at the base of the disc.

Habitat.—The type was collected along "a swift running stream at the base of the vertical wall of Marahuaca. Conditions, upper tropical but vegetation is not thick and the trees not high. Collections from about 1,200 m" (Rivero, 1961:183). UPRM 2869 was collected close to large, moss-covered rocks of a nearly dry creek at an elevation of 612 m (Rivero, 1972:187).

Distribution.—The species is known from two localities in southern Venezuela: 1200 m on Cerro Marahuaca and 610 m on Cerro Duida (Fig. 2).

Remarks.—When describing this species, Rivero (1961:118) realized he was dealing with a rather aberrant taxon, which he provisionally described in *Hyla*. But he mentioned the *Eleutherodactylus*-like habitus and the fact that the first finger was longer than the second, a reason for him to point out its probable relationship with *Gastrotheca*. In 1968 Rivero apparently had not yet decided about its generic allocation because he alternately called the species *Hyla marahuacensis* or *Stefania marahuacensis*, stating on p. 140 that its morphological characters clearly relate it to *Stefania*, followed by the statement that it belongs in the *Stefania evansi* group. Considering a suggestion by C. J. Goin that *S. marahuacensis* might be a juvenile *S. evansi*, Rivero (1968:145) stated: "Indeed, the animal is probably a young *Stefania*." In 1971 Rivero treated the species as a member of *Stefania* without reservation. The characteristic pustular condition of the tympanic area of *Stefania* reaches an extreme in this species. The tubercles, which in the other known species are flat or rounded, are coneiform in *S. marahuacensis*. This species is considerably smaller than other species of the genus, although the size of adult females still remains unknown. The differences between the two known specimens mentioned by Rivero (1972:187), seem to be of trivial importance. They can be explained by size differences and are



ERRATUM for "The taxonomy and phylogenetic relationships of the hylid frog genus Stefania." Univ. Kansas Mus. Nat. Hist. Misc. Publ., 75. 1984.

INSERT the following caption at the bottom of the second column on page 22:

Fig. 20.-- Color pattern of holotype of Stefania marahuaquensis, MCZ 28566, juv. ♂. Line = 10 mm.

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completely within the normal range of variation known for other species of *Stefania*.

Stefania riae new species

Stefania sp. "B" Hoogmoed, 1979:272.

Holotype.—KU 174688, an adult female from Cerro Sarisariñama, 1400 m, Estado Bolívar, Venezuela, collected by P. Bermudes.

Paratypes.—KU 174689, an adult male, same data as holotype; USMN 212331, Cerro Sarisariñama.

Diagnosis.—A large *Stefania*, females attaining a snout-vent length of 59 mm; the single available male, 56 mm; head as wide as long or slightly longer; frontoparietal ridges indistinct; canthus rostralis distinct, angular, concave. Tympanum more than half diameter of eye. First finger slightly longer than second; discs well developed on all fingers and toes. Toes webbed basally. Skin on dorsum shagreened, lacking bold pattern.

Description.—Head as wide as long or slightly longer, distinctly wider than adjacent part of body; depth slightly less than half length. Snout ovoid in dorsal view, rounded in profile, short, but distinctly longer than horizontal diameter of eye. Distance between eye and nostril slightly shorter than horizontal diameter of eye, distinctly more than twice the distance between nostril and tip of snout. Canthus rostralis distinct, angular, concave, with several knobs on its posterior half; loreal region distinctly concave, gradually sloping to the unflared lips. Nostrils protuberant, directed laterally and slightly posterodorsally in slightly swollen areas immediately below canthus rostralis. Distance between nostrils 60–70% of interorbital distance, 1.2–1.6 times distance between nostril and tip of snout; area between nostrils slightly concave. Interorbital space concave, slightly wider than upper eyelid. Frontoparietal ridges indistinct. Temporal region sloping steeply. Tympanum distinct, surrounded by a bony annulus, large, round, more than half horizontal diameter of eye, separated from eye by a distance slightly more than half its diameter. Supratympanic fold distinct anteriorly, curved, extending from posterior corner of eye just above insertion of

forelimb, obscuring upper edge of tympanum (Fig. 21).

Choanae large, oval or slit-like. Pre-vomerine processes large, transverse, between choanae, bearing 5–8 teeth each. Tongue large, round. Pupil horizontally oval. Palpebral membrane not reticulated, with a brown pigmented zone along its upper rim.

Skin on dorsum, upper eyelids, throat, flanks, and limbs shagreened. Dorsal surface of snout and loreal region with larger pustules. Temporal region and area posteroventral to tympanum with rounded warts. Belly finely granular. Anteroventral surface of thighs smooth. Anal opening directed posteriorly at upper level of thighs.

Pollical tubercle large, distinct, oval; palmar tubercle large, distinct, deeply bifid. Subarticular tubercles single, large, distinct, round. Supernumerary tubercles present on palm and base of fingers, large, flat. First finger longer than second, shorter than fourth, third longest. Third and fourth fingers fused at their base, apparently forming an operational unit that is opposable to first and second fingers. Fingers completely devoid of webbing. Discs on fingers large, transversely oval to triangular, wider than penultimate phalanx, largest on fourth finger (approximately three-fourths of tympanum diameter, or covering about half of tympanum). Both males having two unpigmented nuptial pads on the first finger—a large irregular one on dorsal surface of distal part of first phalanx, and a small, oval one on dorsal surface of pollical tubercle (Fig. 22).

Inner metatarsal tubercle large, distinct, oval; outer metatarsal tubercle small, distinct, round. Subarticular tubercles single, large, round, distinct. Supernumerary tubercles present on base of toes, small, flat. Third toe slightly shorter than fifth. Toes basally webbed. Webbing formula: I2–2¹/₂ II(1³/₄–2)–3III(2–2¹/₂)–3¹/₂IV(3¹/₃–3¹/₂)–(2–2¹/₃)V. Discs on toes large, smaller than those on fingers, oval to triangular, distinctly wider than penultimate phalanx. When hindlimbs folded and flexed at right angles to sagittal plane of the body, the heels overlap considerably.

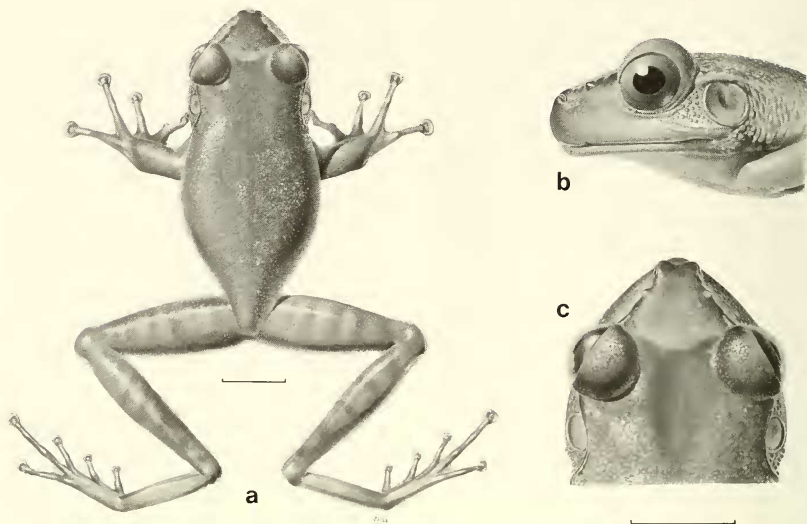


FIG. 21.—Holotype of *Stefania riae*, KU 174688, ♀. a. Dorsum. b. Lateral view of head. c. Dorsal view of head. Lines = 10 mm.

No data on color of living specimens are available.

In preservative, the dorsum is brown with an indistinct, irregular pattern of dark brown spots in the holotype and USNM 212331. In KU 174689 the pattern on the back is more distinct and has two paler dorsolateral lines, which fade on the posterior part of the back. An indistinct paler vertebral line and faint interorbital bar are present. The limbs have transverse brown bars on a pale brown ground color. The venter is white to pale brown with a few brown spots on the throat.

Distribution.—This species is known only from the type locality, the plateau on top of Cerro Sarisariñama, Estado Bolívar, Venezuela, at an elevation of 1400 m (Fig. 2).

Etymology.—This species is named for Ria Hoogmoed-Verschoor, spouse of MSH, in recognition of the help and encouragement she provides and for her understanding attitude when fieldwork necessitates long absences of her husband.

Stefania roraimae new species

Stefania sp. "A" Hoogmoed, 1979:272.

Holotype.—UGDB 10, an adult female,

from Roraima, Guyana, 1402 m, collected by M. Tamessar on 24 October 1973.

Diagnosis.—A medium-sized *Stefania*; the single available female attaining a snout-

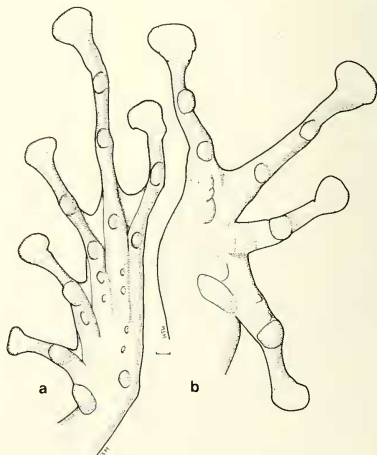


FIG. 22.—Foot (a) and hand (b) of *Stefania riae*, KU 174688, ♀. Line = 1 mm.

vent length of 46 mm; head slightly longer than wide, frontoparietal ridges indistinct; canthus rostralis distinct, angular, concave. Tympanum less than half diameter of eye. First finger much longer than second; discs well developed on fingers, small on toes. Toes webbed basally. Skin on back smooth, with bold pattern of wide, pale interorbital bar, dorsolateral stripes, and pale spots on belly and legs.

Description.—Head slightly longer than wide, distinctly wider than adjacent part of body; depth slightly less than half length. Snout ovoid in dorsal view, rounded in profile, short, slightly longer than horizontal diameter of eye. Distance between eye and nostril distinctly shorter than horizontal diameter of eye, slightly less than twice distance between nostril and tip of snout. Canthus rostralis distinct, angular, concave; loreal region distinctly concave, gradually sloping to unflared lips. Nostrils not protuberant, directed laterally below the canthus rostralis. Distance between the nostrils four-fifths interorbital distance, about 1.5 times distance between nostril and tip of snout; area between nostrils flat. Interorbital space flat, about as wide as upper eyelid. Upper eyelid smooth. Frontoparietal ridges indistinct. Temporal region sloping steeply. Tympanum distinct, large, round, nearly half horizontal diameter of eye, separated from eye by a distance equal to its diameter. Supratympanic fold distinct, straight, horizontal, extending from posterior corner of eye to just posterior to tympanum, obscuring upper edge of tympanum (Fig. 23).

Choanae large, oval. Prevomerine processes large, positioned transversely between anterior margins of choanae, bearing 5–6 teeth each. Tongue large, round. Pupil horizontally oval. Palpebral membrane not reticulated, with a brown pigmented zone along its upper rim.

Skin on dorsum, throat, flanks and legs smooth. Skin on belly indistinctly shagreened. Temporal region with distinct rounded warts. Anal opening directed posteriorly at upper level of thighs.

Pollical tubercle large, distinct, oval; palmar tubercle large, distinct, bifid. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles absent.

First finger much longer than second, shorter than fourth; third longest. First and second fingers apparently forming an operational unit that is opposable to third and fourth fingers, which are fused at their base. Fingers completely devoid of webbing. Disc on first finger small, approximately round, as wide as penultimate phalanx; discs on other fingers large, oval, wider than penultimate phalanx, largest on third and fourth fingers (approximately one-third diameter of tympanum).

Inner metatarsal tubercle large, distinct, oval; outer metatarsal tubercle small, distinct, round. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles absent. Third toe shorter than fifth. Toes basally webbed; webbing formula: $I2-2\frac{1}{2}II2-3III2\frac{1}{2}-3\frac{3}{4}IV3\frac{1}{2}-(2-2\frac{1}{2})V$. Discs on toes small, round to oval, hardly wider than the penultimate phalanx, smaller than discs on fingers. When hindlimbs folded and flexed at right angles to sagittal plane of body, heels overlap considerably.

No data are available on the color of the living specimen.

In preservative, the dorsum is brown with a whitish interorbital bar, connected on the upper eyelids with whitish dorsolateral stripes. The flanks are brown with a series of whitish, round spots along the lower part. The thighs and feet are brown with irregularly shaped whitish spots. The forelimbs have oblique transverse pale and dark brown bands. A large white spot is present in the loreal region. The throat is pale brown with paler brown spots. The belly is pale brown with whitish spots. The ventral surfaces of the thighs, shanks, and forelimbs are brown with irregularly shaped whitish spots (Fig. 24).

Distribution.—The species is known only from the type locality, the northern slopes of Mount Roraima, where it occurs at an altitude of 1402 m (Figs. 2, 15).

Stefania woodleyi Rivero

Stephania woodleyi Rivero, 1968:147 [Holotype.—BMNH 1967:654 from Mount Kanaima near Potaro River, Guyana].

Stefania woodleyi Rivero, 1970:467; Gorham, 1974:112; Lescure, 1975:78, 1977:

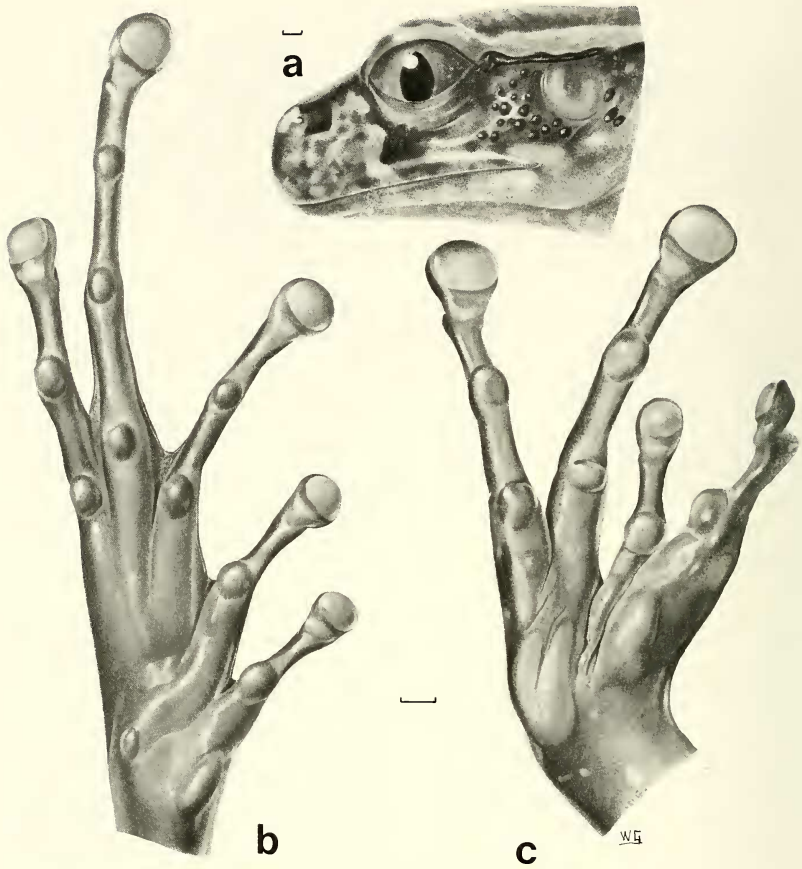


FIG. 23.—Holotype of *Stefania roraimae*, UGDB 10, ♀. a. Side of head. b. Foot. c. Hand. Lines = 1 mm.

61; Duellman, 1977:182; Hoogmoed, 1979:256, 272.

Diagnosis.—A large *Stefania*; the single known female having a snout-vent length of 61 mm; head slightly longer than wide; frontoparietal ridges absent; canthus rostralis distinct, angular, straight. Tympanum slightly less than half diameter of eye. First finger distinctly longer than second; discs well developed on all fingers and toes. Toes webbed basally. Skin on dorsum distinctly granular with bold reticulated pattern.

Description.—Head slightly longer than wide, slightly wider than adjacent part of body, depth distinctly less than half of length. Snout subovoid in dorsal view, rounded in profile; distinctly longer than horizontal diameter of eye. Distance between eye and nostril about one-third shorter than horizontal diameter of eye, more than twice distance between nostril and tip of snout. Canthus rostralis distinct, angular, straight, with smooth edge. Loreal region distinctly concave, gradually sloping to unflared lips. Nostrils barely protuberant, di-

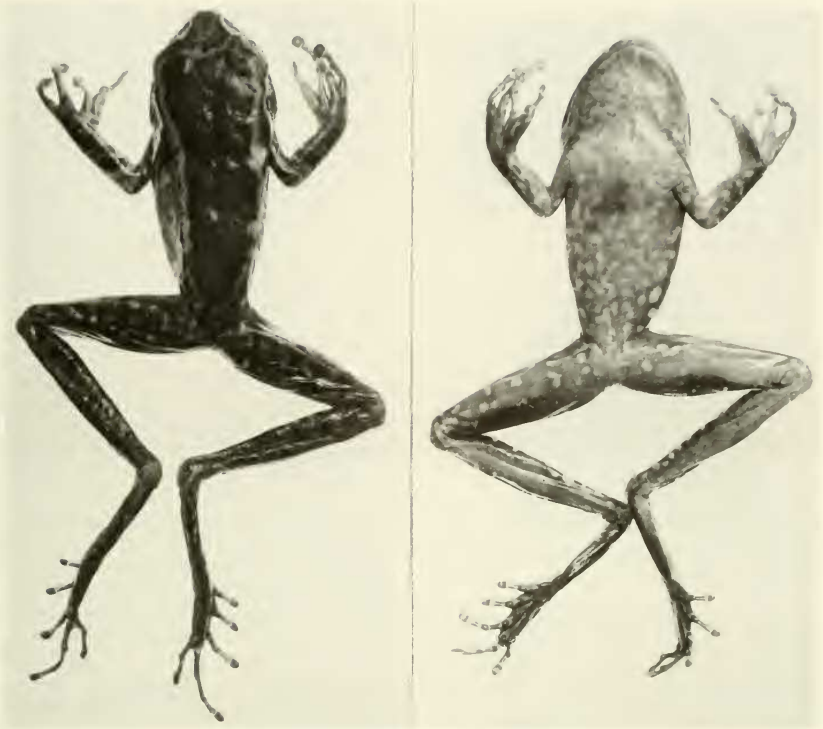


FIG. 24.—Holotype of *Stefania roraimae*, UGDB 10, ♀.

rected laterally and slightly anteriorly below canthus rostralis. Distance between nostrils 54% of interorbital distance, 1.2–1.3 times distance between nostril and tip of snout; area between nostrils flat. Interorbital space flat, distinctly wider than upper eyelid. Frontoparietal ridges absent. Temporal region sloping very steeply, nearly vertical. Tympanum distinct, surrounded by a bony annulus, large, round, slightly less than half horizontal diameter of eye, separated from eye by a distance three-fourths of its diameter. Supratympanic fold distinct anteriorly, curved, extending from posterior corner of eye to just above insertion of forelimb, obscuring part of upper edge of tympanum (Fig. 25).

Choanae large, oval. Prevomerine processes large, transverse between choanae, each bearing 6–8 teeth. Tongue large,

round, slightly indented posteriorly. Pupil horizontally oval. Palpebral membrane not reticulated, with a brown pigmented zone along its upper rim.

Skin on dorsum, top of head (including upper eyelids), loreal region, flanks and belly granular. Skin on throat, chest, and ventral surfaces of limbs smooth. Skin on dorsal surfaces of limbs shagreened. Temporal region and area posteroventral to tympanum with rounded warts. The loose lateral folds mentioned in the original description seem to be an artifact of preservation. Anal opening at upper level of thighs, directed posteriorly and slightly ventrally, with short, transverse supra-anal sheath.

Pollical tubercle large, distinct, oval; palmar tubercle large, distinct, deeply bifid. Subarticular tubercles single, large, distinct, round. Supernumerary tubercles absent.

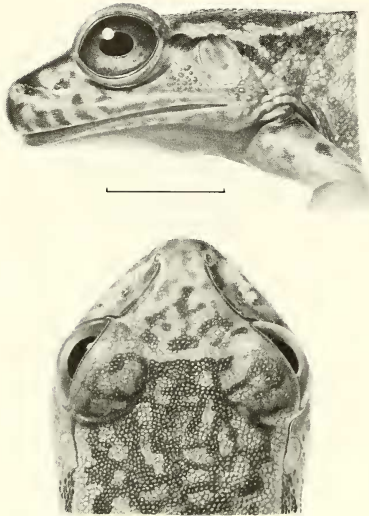


FIG. 25.—Holotype of *Stefania woodleyi*, BMNH 1967.654, ♀. Line = 10 mm.

First finger distinctly longer than second, shorter than fourth, third longest. Third and fourth fingers fused at base, forming an operational unit apparently opposable to first and second fingers. Fingers completely devoid of webbing. Discs on fingers large, transversely oval to round, wider than penultimate phalanx, largest on fourth finger (approximately half of diameter of tympanum) (Fig. 26).

Inner metatarsal tubercle large, distinct, oval; outer metatarsal tubercle smaller, distinct, round. Subarticular tubercles single, large, round, distinct. Supernumerary tubercles absent. Third toe distinctly shorter than fifth. Toes webbed basally; webbing formula: $I(2-2\frac{1}{4})-2\frac{1}{2}II2-3III2\frac{1}{2}-3\frac{2}{3}IV3\frac{2}{3}-2\frac{1}{3}V$. Discs on toes large, smaller than those on fingers, round to triangular, distinctly wider than penultimate phalange. When hindlimbs folded and flexed at right angles to sagittal plane of body, heels overlap considerably.

No data are available on color of living specimens.

In preservative, the dorsum is brown with a very distinct pattern of ochre-colored,

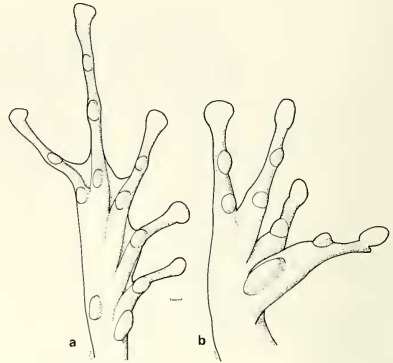


FIG. 26.—Foot (a) and hand (b) of *Stefania woodleyi*, BMNH 1967.654, ♀. Line = 1 mm.

irregularly dispersed and shaped spots, transverse interorbital bar and dorsolateral stripes. The side of the head is ochre with a dark brown canthal stripe and brown spots on the upper lips. A dark brown to blackish supratympanic stripe is present. The dorsal part of snout anterior to the interorbital bar is ochre with brown spots. The groin and anterior surfaces of the thigh are dark brown with several white spots in the groin. The dorsal surfaces of the limbs have dark brown transverse bars—six on the thighs and six or seven on the shanks. The posterior surfaces of the thighs are dark brown with scattered pale spots. The tarsi are ochre with brown spots. The venter is pale brown with indistinct whitish mottling (Fig. 27).

Habitat.—The few data accompanying the



FIG. 27.—Holotype of *Stefania woodleyi*, BMNH 1967.654, ♀, 61 mm snout-vent length.

holotype indicate that it came from a rocky stream on the slope of Mount Kanaima, near the Potaro River. A more extensive description of the habitat is provided by Goin and Woodley (1969).

Distribution.—The species is known only from the type locality, Mount Kanaima, Guyana, where it occurs at an elevation of 700 m (Figs. 2, 15).

Remarks.—*Stefania woodleyi* is sympatric

with *S. evansi*, although it is not certain that both species are syntopic. Possibly in areas where they occur in sympatry, *S. woodleyi* prefers steeper parts with fast-flowing creeks, whereas *S. evansi* might prefer flat areas with more sluggish streams. The two species are easily discernable on the basis of the basally webbed toes (fully webbed in *S. evansi*), granular skin (shagreened in *S. evansi*), adult size (larger in *S. evansi*) and color pattern.

PHYLOGENETIC RELATIONSHIPS

INTRAGENERIC RELATIONSHIPS

Although numerous taxonomic characters, such as sizes, proportions, coloration, and skin texture are available to define the species, far fewer characters can be utilized in a phylogenetic construct. These are characters for which evolutionary direction can be inferred with a reasonable degree of certainty. These characters are defined below with their character states and polarity indicated, and the distribution of the character states among the species of *Stefania* and in the outgroup (*Cryptobatrachus*) are given in Table 2.

A. Relative lengths of first and second fingers. The first finger being longer than the second seems to be a specialization for arboreality among egg-brooding hylids.

Finger 1 < finger 2 = 0

Finger 1 > finger 2 = 1

0 → 1

B. Prevomerine dentigerous processes. The association of the dentigerous processes of the prevomers with the palatines is a

feature unique to *Cryptobatrachus*, whereas the more anterior position of the processes in *Stefania* is like the condition in most hylids.

Processes anterior to palatines = 0

Processes associated with palatines = 1

0 → 1

C. Frontoparietal ridges. The lateral edges of the frontoparietals may be slightly to greatly elevated in hylids having the skull roof heavily ossified (Trueb, 1973).

Ridges absent = 0

Ridges weak = 1

Ridges prominent = 2

0 → 1 → 2

D. Anterior ramus of the squamosal. The squamosal usually is ligamentously attached to the maxillary, but in anurans with extensive cranial ossification the anterior ramus of the squamosal forms a bony arch connecting with the maxillary (Trueb, 1973).

Squamosal not extending to maxillary = 0

Squamosal extending to maxillary = 1

0 → 1

E. Transverse processes of vertebrae. Among hylids the breadth of the transverse processes usually is less than the width of the sacrum; broad processes usually are associated with terrestriality (Trueb, 1973).

Transverse processes < sacrum = 0

Transverse processes = sacrum = 1

0 → 1

F. Relative width of head. Anuran skulls generally are longer than wide. Increased width, relative to length, usually is associated with cranial modifications including increased ossification.

Width < length = 0

Width > length = 1

0 → 1

TABLE 2.—Distribution of character states in *Cryptobatrachus* and among the species of *Stefania* (See text for definition of characters)

| Taxa | Characters | | | | | | | | |
|--------------------------|------------|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I |
| <i>S. evansi</i> | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>S. ginesi</i> | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>S. goini</i> | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 | 0 |
| <i>S. marahuacuensis</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 |
| <i>S. riae</i> | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| <i>S. roraimae</i> | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>S. woodleyi</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Cryptobatrachus</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

G. Exostosis. Sculpturing of the cranial roofing bones is a derived feature (Trueb, 1973). Exostosis:

- Absent = 0
- Weak = 1
- Moderate = 2
- 0 → 1 → 2

H. Eyelid tubercles. Dermal modifications of the eyelids occur sporadically among hylid frogs. They are generally considered to be derived characters.

- Tubercles absent = 0
- Tubercles present = 1
- Dermal flap = 2
- 0 → 1 → 2

I. Post-tympanic tubercles. The skin behind the tympanum usually is smooth in hylid frogs. Derived character states are low, flat tubercles and conical tubercles.

- Tubercles low = 0
- Tubercles conical = 1
- 0 → 1

The character states of the various taxa were analyzed by cladistic methods using the WAGNER 78 program implemented on the Honeywell 66/60 computer at the University

of Kansas by J. S. Farris. For the methodology of computation, see Farris (1970), and for the general philosophy of the cladistic methodology, see Wiley (1981). By entering taxa into the program in different sequences, 15 phylogenetic trees were generated, but these manipulations resulted in only one arrangement—a tree having 14 steps and one reversal in character E (transverse processes of the vertebrae) and one convergence in character H (eyelid tubercles) (Fig. 28).

The reversal in character E (transverse processes of the vertebrae) occurs on the branch including *S. ginesi* and *S. goini*, both of which possess derived states of characters D (anterior ramus of squamosal) and F (relative width of head). There is little doubt that these two species are closely related and derived from a more generalized stock of *Stefania*. Eyelid tubercles (character H) are considered to be independently derived in *S. riae* and *S. marahuaquensis*. In the latter there is a dermal flap on the eyelid; this is considered to be a secondarily derived state of character H. *Stefania marahuaquensis* is unique in possessing conical post-tympanic

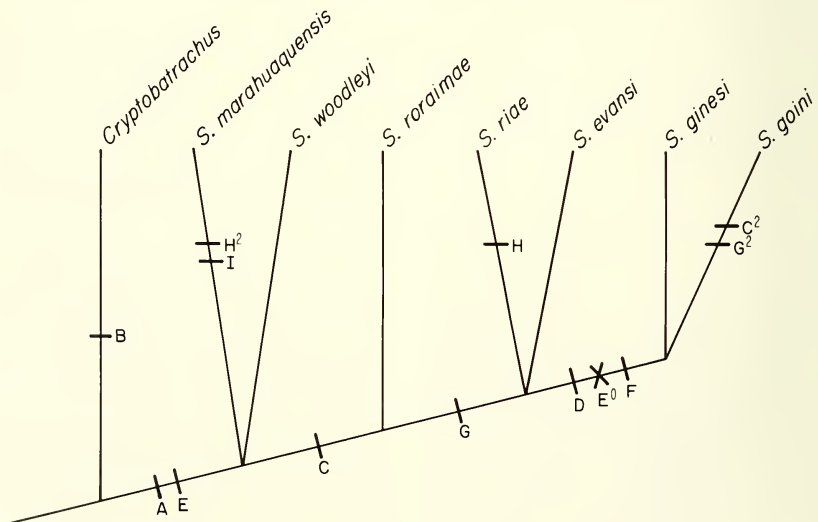


FIG. 28.—A phylogenetic tree generated by the WAGNER 78 program. Diagonal bars indicate internodal shifts in character states; the X indicates a reversal in a character state. Letters refer to the characters defined in the text (character states tabulated in Table 2). Superscripts on letters by diagonal bars indicate shifts to secondarily derived character states; superscript on letter by the X indicates the character state after reversal.

warts. The correlation of increased dermal modification on the eyelid and in the post-tympanic region may be expressions of a single gene in *S. marahuaguensis*. Additional characters are necessary to resolve the trichotomies involving *S. marahuaguensis-woodleyi* and *S. riae-evansi* lineages.

RELATIONSHIPS WITH *CRYPTOBATRACHUS*

Historically, *Stefania* and *Cryptobatrachus* have been considered to be not only similar to one another but also sister groups. In fact, the morphological character states used to separate the two genera are not particularly impressive when compared with the variation within many genera of hylids, such as *Gastrotheca*. Although characters, such as the relative lengths of fingers and toes, size of choanae, extent of ossification of the sphenethmoid, relative positions of prevomerine dentigerous processes (Fig. 1), and presence or absence of vocal slits, separate all species of *Stefania* from all *Cryptobatrachus*, the differences in these characters, individually or in combination, do not seem to warrant the recognition of two genera. Limited karyological data on *Stefania evansi* and *Cryptobatrachus boulengeri* provided by James P. Bogart show only minor differences. In both genera there are five pairs of macrochromosomes and eight pairs of microchromosomes. The chromosomes are all metacentric or submetacentric, except for chromosome 5 in *Stefania* and chromosome 12 in *Cryptobatrachus*, which are subtelocentric; the first two chromosomes of *Stefania* are somewhat longer than their counterparts in *Cryptobatrachus* (Table 3; Fig. 29).

On the other hand, embryos of *Stefania* and *Cryptobatrachus* differ in the number of pairs of external gills and in the extent of coverage by the gills. The two pairs of gills in *Stefania* completely envelope the embryo, whereas in *Cryptobatrachus* the single pair of gills covers only the dorsal part of the embryo. This difference in gills is impressive when viewed in the context of variation in external gills in egg-brooding hylids (del Pino and Escobar, 1981). Results of a quantitative immunological comparison by microcomplement fixation of an albumin

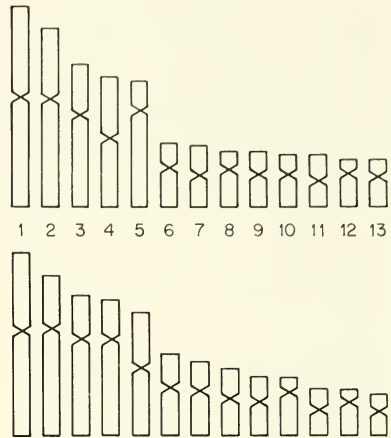


FIG. 29.—Idiograms of chromosomes of *Stefania evansi* (KU 181112) above and *Cryptobatrachus boulengeri* (J. P. Bogart 5456) below.

sample of *Stefania evansi* with the antiserum of *Cryptobatrachus boulengeri* gave an immunological distance of approximately 150 units (L. R. Maxson, pers. comm.). This is far greater than the distances between *Stefania* and *Gastrotheca* or *Cryptobatrachus* and *Gastrotheca* (Scanlan et al., 1980).

Thus *Stefania* and *Cryptobatrachus* have undergone a great amount of biochemical evolution with little morphological divergence. The high degree of independence of molecular and morphological evolution was stressed by Wilson et al. (1974) and noted in egg-brooding hylids by Scanlan et al. (1980). Whereas chromosomal and regulatory evolution seem to be important in the control of organismal evolution, time alone seems to be the major factor in protein evolution (Wilson et al., 1974, 1977). Albumin evolution apparently proceeds in a clocklike fashion (Sarich and Wilson, 1967; Maxson, 1977; Maxson et al., 1979); according to the calculations by Wilson et al. (1977), 100 units of immunological distance accumulate every 55 million years of separation. On the basis of this calculation we estimate that *Stefania (evansi)* and *Cryptobatrachus (boulengeri)* diverged about 82 million years ago in the late Cretaceous. If this time estimate is anywhere nearly cor-

TABLE 3.—Comparative chromosome structure in *Stefania evansi* (Stef.) and *Cryptobatrachus boulengeri* (Cryp.)

| Species | Character | Chromosome number | | | | | | | | | | | | |
|---------|-----------|-------------------|-------|-------|-------|-------|------|------|------|------|------|------|------|------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| Stef. | % Length | 16.31 | 14.53 | 11.68 | 10.51 | 10.26 | 5.29 | 5.18 | 4.72 | 4.69 | 4.43 | 4.43 | 4.03 | 3.94 |
| | Ratio | 1.23 | 1.56 | 1.81 | 1.20 | 3.47 | 1.72 | 1.13 | 2.11 | 1.50 | 1.77 | 1.08 | 2.80 | 2.24 |
| | Index | 0.45 | 0.39 | 0.36 | 0.45 | 0.22 | 0.37 | 0.47 | 0.32 | 0.40 | 0.36 | 0.48 | 0.26 | 0.31 |
| | Type | m* | m | sm | m | st | sm | m | sm | m | sm | m | sm | sm |
| Cryp. | % Length | 14.92 | 13.03 | 11.39 | 11.09 | 10.12 | 6.72 | 6.05 | 5.56 | 4.99 | 4.87 | 3.99 | 3.78 | 3.49 |
| | Ratio | 1.29 | 1.98 | 2.19 | 2.40 | 1.25 | 1.42 | 1.51 | 1.20 | 1.33 | 2.82 | 1.22 | 3.13 | 1.52 |
| | Index | 0.44 | 0.34 | 0.31 | 0.29 | 0.44 | 0.41 | 0.40 | 0.45 | 0.43 | 0.26 | 0.45 | 0.24 | 0.40 |
| | Type | m | sm | sm | sm | m | m | m | m | m | sm | m | st | m |

* m = metacentric; sm = submetacentric; st = subtelocentric

rect, despite lengthy separation, the two genera have diverged morphologically very little, and the major differences that developed subsequent to their separation involved the number and sizes of the gills covering the embryos.

RELATIONSHIPS WITH OTHER AMPHIGNATHODONTINAE

Egg-brooding hylids have been separated from other hylids as the subfamily Amphignathodontinae, except that the bizarre *Hemiphraactus* has been recognized as a separate subfamily (Duellman, 1970; Trueb, 1974). For the purposes of this discussion all of the genera will be considered as amphignathodontines.

Studies of gill development and pouch structure (del Pino, 1980; del Pino and Escobar, 1981) have provided some of the most meaningful data for determining the phylogeny of the amphignathodontines. A sequential structural complexity of pouch types exists: *Gastrotheca* has numerous pouch types, all of which are more complex than those in *Flectonotus* and *Fritziana*; the simplest arrangement is no pouch at all, as in *Stefania*, *Cryptobatrachus*, and *Hemiphraactus*. *Stefania* and *Hemiphraactus* are alike in having two pairs of large gills that completely envelop the embryo, which develops directly into a froglet. Two pairs of gills also are present in *Fritziana*, but embryos of these have gills covering less than one-quarter of their surface and hatch as non-feeding tadpoles that complete their development in bromeliads and subsist on a residue of yolk. *Flectonotus* is like *Fritziana* in development and gill coverage, except that

only one pair of gills is present. *Cryptobatrachus* has only one pair of gills that cover less than half of the embryo, which hatches into a froglet. *Gastrotheca* and *Amphignathodon* have only one pair of gills that entirely covers the embryo, but these gills are the result of the fusion of two pairs of gills, as evidenced by the presence of two gill stalks per gill in many taxa. The developing embryos of *Gastrotheca* hatch as feeding tadpoles or froglets, and those of *Amphignathodon* hatch as froglets.

An hypothesized phylogeny of the amphignathodontine genera (Fig. 30) has an unresolved trichotomy involving *Hemiphraactus* and the branch to *Stefania* and *Cryptobatrachus*. Otherwise, it is a parsimonious cladogram containing no reversals and three convergences.

Some explanation is required of the polarity of certain character states and the variation in character states in some genera. As used here, *Flectonotus* includes only two species—*F. fitzgeraldi* and *F. pygmaeus* in Venezuela and continental islands; *F. fissilis* in southeastern Brasil seems to be more closely allied with the two species of *Fritziana* in the same region (Duellman and Gray, 1983). The gills in *Hemiphraactus fasciatus* are fused as they are in *Gastrotheca*; other species of *Hemiphraactus* have two distinct pairs of gills enveloping the embryos. Some species of *Gastrotheca* have only one pair of stalks to their gills. This is interpreted as a loss of stalks subsequent to fusion of the gills (del Pino and Escobar, 1981).

The most complex pouches are in species of *Gastrotheca* having eggs that hatch as

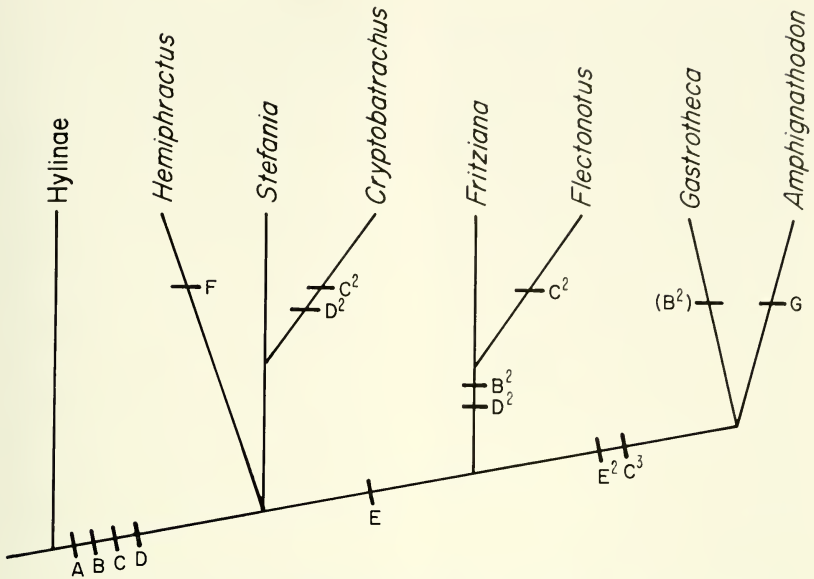


FIG. 30.—Hypothesized phylogenetic relationships of amphignathodontine hylids, which differ from hylines by the following derived character states: A. Egg-brooding; B. Direct development; C. Two pairs of large external gills; and D. Gills covering entire embryo. Primitive genera (*Hemiphractus*, *Stefania*, and *Cryptobatrachus*) have no dorsal pouch. An open dorsal pouch (E) is a derived character state characterizing all marsupial frogs (*Fritiziana*, *Flectonotus*, *Gastrotheca*, and *Amphignathodon*); the last two genera have closed pouches (E²), a secondarily derived character state. In addition to numerous morphological peculiarities, *Hemiphractus* is distinguished from other amphignathodontines by having fanglike teeth (F). *Amphignathodon* differs from *Gastrotheca* (and all other frogs) by having mandibular teeth (G). The anterior pair of gills is lost (C²) in *Cryptobatrachus* and *Flectonotus*, and the gills cover only part of the embryo (D²) in *Cryptobatrachus* (<50% coverage) and the branch leading to *Fritiziana* and *Flectonotus* (<25% coverage). An independently derived state of one pair of gills (C³) is accomplished by fusion of the two pairs. Although direct development of eggs into froglets is a derived character state unifying the amphignathodontines, feeding tadpoles are produced by some species of *Gastrotheca*, and nonfeeding tadpoles are characteristic of *Fritiziana* and *Flectonotus* (B²). See text for justification of tadpoles being derived and for further explanation of characters.

tadpoles. Furthermore, all *Gastrotheca* have highly derived gills. These facts led del Pino (1980) and del Pino and Escobar (1981) to suggest that tadpoles are derived in *Gastrotheca*. This suggestion was supported by Scanlan et al. (1980), who found that the species of *Gastrotheca* that produce tadpoles are immunologically close to one another and to some species that have direct development. The arrestment of embryonic development may be an adaptation for harsh environments (above tree-line in the Andes) in *Gastrotheca*, and the hatching of eggs as nonfeeding tadpoles in *Fritiziana* and *Flectonotus* may be forced upon these small frogs simply by size constraints.

Structurally and reproductively *Stefania* seems to be the most primitive living group of amphignathodontine hylids. Its antiquity is suggested by the great immunological distance between *Stefania* and *Cryptobatrachus*.

BIOGEOGRAPHY

On the basis of the immunological distance calculated between *Stefania* and *Cryptobatrachus*, we can assume that the divergence of the egg-brooding hylids that lack pouches may have occurred prior to the Late Cretaceous. *Stefania* is endemic to the Guiana Shield, and there is no evidence that it ever occurred anywhere else. Thus, our

discussion of the biogeography of *Stefania* emphasizes the history of the Guiana Shield, a region, together with the Brazilian Shield, that is formed primarily of Proterozoic sandstones (Priem et al., 1973). These two regions have been continuously emergent throughout the Mesozoic, Tertiary, and Quaternary. The shields presumably were continuous with one another until the Late Cretaceous when both were elevated, and the subsidence of the Amazon Basin was initiated; both shields were uplifted farther in the Tertiary (Beurlen, 1970; Valetón, 1973). The table mountains (tepui) of the Guiana Shield are erosional remnants of the Cretaceous and Tertiary uplifts (Haffer, 1974). Most of the tepuis have flat tops and perpendicular cliffs several hundred meters high separating the summits from talus at the bases of the cliffs. With the exception of *S. evansi*, all species of *Stefania* are restricted to the tops or slopes of the tepuis. Hoogmoed (1979) discussed the application of various theories of the origin of the fauna of the tepuis and concluded that highland endemics, such as *Stefania*, best fit the "plateau theory," which is based on the geological evidence that a more extensive tableland existed on the Guiana Shield during the Mesozoic and Tertiary, prior to intensive erosional dissection. This model necessitates the differentiation of *Stefania* from other egg-brooding hylids prior to the uplift in the Late Cretaceous, and this timing is supported by the estimated time of divergence of *Stefania* and *Cryptobatrachus* at 82 million years ago on the basis of immunological distance.

The erosional dissection of the tableland resulted in the fragmentation of the continuous high elevations into the numerous tepuis—continental islands, each harboring isolated populations of organisms on their summits or slopes. The area of the western tepuis, which includes Cerro Duida, Cerro Marahuaca, and Cerro Sarisariñama, is more deeply dissected, with resulting greater isolation of the tepuis, than the central and eastern area; in this area, which contains Chimantá-tepui, Auyán-tepui, Mount Roraima, and Mount Kanaima, the tepuis are less isolated from one another, for many are connected by ridges at elevations

of about 1000 m. It is unknown for certain whether erosion of the area began earlier or proceeded faster in the west than in the east. However, present rainfall is heavier in the west—3300–3500 mm annually on western tepuis as compared to 2000–2500 mm on the eastern tepuis (Snow, 1976). Thus, it seems most likely that this region of one orogenic history has been dissected at different rates because of higher precipitation in the west.

Climatic fluctuations, especially during the Pleistocene, may have had significant effects on altitudinal climatic zonation in the Guiana highlands. Results of palynological investigations indicate that temperatures during glacial times were at least 3° C lower in the coastal lowlands than they are today (van der Hammen, 1974); this would depress climatic zones in the highlands by at least 300 m. Furthermore, during glacial times, rainfall decreased, so much so that savannas and grassland expanded at the expense of forests in the lowlands (Wijmstra and van der Hammen, 1966), but moist forest remained on the slopes of the highlands (Haffer, 1974).

Some aspects of the phylogenetic arrangements of the species of *Stefania* are consistent with the hypothesis that the tepuis are erosional remnants of a former plateau that eroded more rapidly in the west than in the east. Among the narrow-headed species comprising the *Stefania evansi* group, *S. marahuacensis* and *S. riae* have uniquely derived character states and exist on isolated tepuis in the western highlands—Cerro Duida-Marahuaca and Cerro Sarisariñama, respectively. Their respective sister species—*S. woodleyi* and *S. evansi* occur in the eastern highlands, as does the independently derived *S. roraimae*.

An early divergence of the *S. goini* group is indicated, because of the isolation of *S. goini* on the western Cerro Duida. We must assume that the ancestral stock inhabited the western and central parts of the highlands prior to their dissection, which resulted in *S. ginesi* being isolated in the Auyán-tepui and Chimantá-tepui region. Alternatively this stock dispersed from the Duida region to the Auyán-tepui region. In the former alternative, the *S. goini* group would have had to have differentiated early in the history of divergence of *Stefania*.

Clearly many aspects of the phylogeny of the species of *Stefania* remain unresolved. More accurate data on the geological history of the tepuis should provide a better means of assessing the possible sequences of orogenies and erosional dissections of the tableland. Furthermore, our knowledge of the herpetofauna of the tepuis is grossly inadequate. Many tepuis have not been investigated. Probably additional species of *Stefania* await discovery. Species in the *Stefania evansi* group are expected to be found on isolated tepuis in eastern Venezuela, whereas additional species of the *Stefania goini* group may be found in the west, such as on Serra de Neblina.

The historical events that resulted in the vicariance of *Stefania* and *Cryptobatrachus* are shrouded in uncertainty. Earlier ideas that the low tablelands between the tepuis and the Andes and including the Sierra de Macarena in Colombia provided an ancient connection between the Guiana Highlands and the Andes have been dispelled by geological evidence that most of the area was below sea level from the Eocene through the Miocene. The table mountains in eastern Colombia probably originated through block faulting in conjunction with the Andean uplift toward the end of the Tertiary and at the beginning of the Pleistocene. As emphasized by Haffer (1974:128): "A high sandstone plateau connecting the southern Venezuelan mesa mountains with the Andes in Colombia or northern Venezuela certainly did not exist at any time during the geological past." The three species of *Cryptobatrachus* have allopatric distributions in moist montane forests at elevations of 1000 to 2550 m in the northern parts of the three Andean cordilleras and in the Sierra Nevada de Santa Marta in Colombia (Duellman, 1979). Prior to the early Pliocene, few areas in the northern Andes were above 1000 m (van der Hammen, 1974; Simpson, 1979). Thus, if *Stefania* and *Cryptobatrachus* differentiated in the Cretaceous, *Cryptobatrachus* must have lived at low elevations at that time. Its restriction to the moist Andean

slopes may be the result of isolation there during dry climatic phases in the late Tertiary and Quaternary.

The historical biogeography of the other amphignathodontine hylids remains to be interpreted. However, it is worthwhile to note that *Hemiphraactus*, the proposed sister group of *Stefania* and *Cryptobatrachus*, inhabits rainforests in the upper Amazon Basin and on the lower Andean slopes. These three genera that brood eggs on the dorsum have allopatric distributions. The presumed most primitive marsupial frogs, *Fritziana*, are endemic to the eastern Brazilian Shield. This distribution is suggestive of differentiation from *Hemiphraactus-Stefania-Cryptobatrachus* lineage in the Cretaceous at the time of the subsidence of the Amazon Basin.

Most other highland endemics among the herpetofauna apparently were derived from lowland ancestors during the Cenozoic. However, two other genera of anurans may be ancient inhabitants of the highlands. The primitive bufonid genus *Oreophrynella* has several species isolated on summits of tepuis (McDiarmid, pers. comm.) and presumably have inhabited the Guiana Highlands since the Cretaceous (McDiarmid, 1971). The monotypic microhylid *Otophyryne* is endemic to the Guianan region, but occurs at low elevations as well as on the plateaus; it possesses a suite of primitive characters (Walker, 1973) and presumably is the most primitive microhylid in the New World.

Our interpretation of the biogeography of *Stefania* coincides with Maguire's (1970) analysis of the flora, of which about 50% of the species are endemic to the Guiana Highlands, and which shows affinities to the flora of the Brazilian Highlands. This is in marked contrast to Mayr and Phelps' (1967) contention that the majority of the avifauna of the Guiana Highlands is relatively young and was derived from the Andean avifauna. Birds are highly vagile and montane species presumably dispersed into the Guiana Highlands during times of climatic depression in the Pleistocene.

SUMMARY

The hylid frog genus *Stefania* contains seven known species. *Stefania riae* is named

from Cerro Sarisariñama, Estado Bolívar, Venezuela, and *S. roraimae* is named from

Mount Roraima, Guyana. *Stefania scalae* Rivero, 1970, is placed in the synonymy of *S. evansi* (Boulenger, 1904). Although size, proportions, coloration, and skin texture are useful taxonomic characters, only nine characters were used to generate a phylogeny of the species. These characters are ones pertaining to osteology, webbing, tuberculation, and finger structure. Five species comprise the *Stefania evansi* group, and two are included in the *Stefania goini* group.

Stefania is one of seven genera of amphignathodontine hylids characterized by brooding eggs on the dorsum or in a dorsal pouch and by having the embryos enveloped in

large external gills. *Stefania* seems to be most closely related to *Cryptobatrachus* in the northern Andes. Although morphologically and karyologically these genera have no major differences, the structure of the embryonic gills is distinctive; immunological evidence suggests that these two genera differentiated in the Cretaceous.

Species of *Stefania* are isolated on tepuis in the Guiana Highlands. Their isolation and subsequent differentiation presumably resulted from erosional dissection of a former continuous highland area into the montane islands that exist today.

RESUMEN

El género de ranas hílidas *Stefania* contiene siete especies conocidos. *Stefania riae* se describe del Cerro Sarisariñama, Estado Bolívar, Venezuela, y *S. roraimae* es descrita de Monte Roraima, Guyana. *Stefania scalae* Rivero, 1970, se coloca en la sinonimia de *S. evansi* (Boulenger, 1904). Aunque el tamaño, las proporciones, la coloración, y la textura de la piel son caracteres con utilidad taxonómica, sólo nueve caracteres fueron utilizados para proponer un modelo de la filogenia de las especies. Estos últimos caracteres corresponden a la osteología, palmeadura, desarrollo de tubérculos, y estructura de los dedos manuales. El grupo *Stefania evansi* comprende cinco especies, y otras dos son incluidas en el grupo de *Stefania goini*.

Stefania es uno de los siete géneros de hílidos anfignathodontinos caracterizados

por incubar huevos en el dorso o en un saco dorsal y por tener los embriones envueltos por grandes branquias externas. *Stefania* parece ser más estrechamente relacionado con *Cryptobatrachus* de los Andes septentrionales. Aunque si bien estos géneros no muestran diferencias mayores en cuando a morfología y cariólogía, la estructura de las branquias embrionarias es distintiva y la evidencia inmunológica sugiere que estos dos géneros se diferenciaron durante el Cretácico.

Los especies de *Stefania* están aisladas en los tepuyes de las montañas de Guayana. Su aislamiento y diferenciación subsecuente probablemente son resultados de la disecación erosiva de un área continua de mesetas que dió lugar a las actuales montañas aisladas.

SPECIMENS EXAMINED

Stefania evansi (59)

GUYANA: Echerak, BMNH 1976.2014-16, 1976.2491, RMNH 18022; Essequibo River, Haiowa Falls, AMNH 49365; Grenada Island, AMNH 18962; Groete Creek, BMNH 1947.2.13.11 (holotype of *H. evansi*); Karisparu, BMNH 1970.583; Kartabo, AMNH 70921; Kurupung River, Makreba Falls, UMMZ 85177; Membaro Creek, upper Mazaruni River, UMMZ 85174-75; Mount Kanaima, Brian's Waterfall, OUM 13479; Mount Kanaima, top, OUM 13501; Mount Roraima, northern

slope, BMNH 1976.2017, 1976.2019; Pipilipai, 50 km E Roraima, BMNH 1976.2012-13; Potaro River, Amatuk Falls, OUM 13535-36; upper Waruma River, foot of Mount Roraima, RMNH 18023.

VENEZUELA: *Estado Bolívar*: La Escalera, El Dorado—Santa Elena de Uairén road, 1050 m, KU 167222-38, 167671 (skeleton), MCZ 64373 (holotype of *S. scalae*), UPRM 2204-05; El Dorado—Santa Elena de Uairén road—km 112, 860 m, KU 167239-56, 167672-74 (skeletons), RMNH 19450, 19454-58; km 114, 900 m, KU

181117; km 116, 950 m, KU 181118-20, 181122-25 (skeletons); km 125, RMNH 19451-53.

Stefania ginesi (7)

VENEZUELA: *Estado Bolívar*: Aprada-tepui, 2450 m, USNM 212044; Auyán-tepui, 2400 m, BMNH 1975.1361-62; Chimantá-tepui, east branch of headwaters of Río Tirica, 2225 m, FMNH 74041 (holotype); Eruda-tepui, north end, 2300 m, USNM 212040; Torona-tepui, 2450 m, USNM 212041-43.

Stefania goini (1)

VENEZUELA: *Territorio Amazonas*: Cerro Duida, Vegas Falls, 1400 m, AMNH 23193 (holotype).

Stefania marahuaguensis (2)

VENEZUELA: *Territorio Amazonas*: Cerro Duida, 612 m, UPRM 2869; Cerro Marahuaca, Cano Cajú, 1200 m, MCZ 28566 (holotype).

Stefania riae (3)

VENEZUELA: *Estado Bolívar*: Cerro Sarisariñama, 1400 m, KU 174688 (holotype), 174689, USNM 212331.

Stefania roraimae (1)

GUYANA: Roraima, 1402 m, UGDB 10 (holotype).

Stefania woodleyi (1)

GUYANA: Mount Kanaima near Potaro River, 700 m, BMNH 1967.654 (holotype).

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